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A STUDY OF THE APPARENT UNEQUAL
SEX RATIO OF WAPITI

by



DONALD R. FLOOK

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SEPTEMBER, 1967

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "A Study of the Apparent Unequal Sex Ratio of Wapiti", submitted by Donald R. Flook in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

This study was conducted to seek the causes of an apparent unbalanced sex ratio favoring females, as observed in wapiti populations in the National Parks in Western Canada and reported from elsewhere.

In the mountainous parks the sex ratio of wapiti older than calves counted in October and November was 37:100. However, as the distribution of females coincided more closely with areas of low elevation and ready access than did that of males, data on sex ratios from those areas are believed biased in favor of females. More reliable population data were obtained from an enclosed 50 square mile area of uniformly low elevation in Elk Island National Park where wapiti were harvested at an average rate of approximately 21 per cent over a 19-year period. During that period the sex ratio in the net production, as represented by the sum of the total harvest and net population change, was 85:100.

The sex ratio of foetuses from all parks in winter was 113:100, and losses of males did not appear to greatly exceed those of females before 1-1/2 years of age. An abrupt decrease in the number of males at low elevations in the mountain parks between 1-1/2 and 2-1/2 years of age, as indicated by the composition of harvests shot by park wardens without deliberate selection, is believed to have been caused by dispersal to other areas. While making males less observable, that dispersal also probably contributes to mortality of males by taking some of them into unfavorable habitats. A marked decline in the number of males after 7 years of age and continuing to 14 years, the oldest represented, is believed due to increased mortality. In contrast, the number of females in successive age classes declined less rapidly, the oldest examined being 21 years of age.

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REIGN OF THE EMPEROR OF THE ROMAN EMPIRE

FROM THE DEATH OF THE EMPEROR JULIUS CAESAR TO THE

DEATH OF THE EMPEROR AUGUSTUS

BY THE REV. JOHN BISHOP, D.D.

IN TWO VOLUMES. THE FIRST VOLUME.

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THE TWENTIETH VOLUME.

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BY

JOHN

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The third part of the paper is devoted to a discussion of the question of the structure of the molecule. It is shown that the structure of the molecule is determined by the laws of quantum mechanics, and that the laws of quantum mechanics are in agreement with the experimental facts.

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INTRODUCTION

Populations of wapiti, *Cervus canadensis* (Erxleben) in several of the National Parks in Canada have increased in the past to levels at which they depleted the stands of winter forage plants, leading to competition with mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) (Clarke, 1942; Cowan, 1947a and 1950; Mair, 1952; Love, 1955; Banfield, 1958; Flook, 1964). For that reason wapiti populations and winter range plant cover have been kept under surveillance, and slaughters by Parks Service personnel have been practiced frequently to control the populations at levels within the carrying capacity of the forage stands. The success of wapiti as a competitor in the National Parks can, no doubt, be attributed, in part at least, to its ability to use a variety of habitat types and forage types (Cowan, 1947; Murie, 1951:188; Morris, 1956; Troyer, 1960; Flook, 1964; Blood, 1966b).

Cowan (1950) reported that during the period 1943 to 1946 when Jasper, Banff, Yoho, and Kootenay National Parks were overstocked with wapiti, the sex ratio among adult wapiti observed was 29 males : 100 females, whereas the sex ratios of the other species of ungulates present more nearly approached equality. Males were also in the minority among adult wapiti removed from Banff and Jasper Parks during that period, in slaughters in which the intention was to take animals non-selectively, as to sex and age.

A deficiency of males, provided it is not so great as to reduce the conception rate, does not lower the rate of increase in a population (Kelker, 1947). As wapiti are polygynous (Murie 1951:126), a deficiency of males could, in circumstances where food is limiting, contribute to sustaining high rates of reproduction and female survival. A knowledge of sex ratios and the factors influencing them is therefore relevant to the problem of

wapiti management in the National Parks.

Kittams (1953) consolidated published and unpublished data on the sexes of wapiti fetuses from Yellowstone National Park and Jackson Hole, U.S.A., and Banff National Park, Canada, and showed that the sex ratio of the composite sample approximated 1:1. The sex ratios of samples of wapiti calves examined soon after birth also approximated 1:1 (Johnson, 1951; Picton, 1961). However, samples of adults observed in various wapiti populations have indicated a marked deficiency of males, usually greater than could be accounted for by selective shooting of bulls. A few examples follow.

The sex ratio of wapiti counted in winter in a lightly hunted population on an over-stocked range in the Olympic Peninsula of Washington as reported by Schwartz (undated) and Schwartz and Mitchell (1945) was 14:100 (males:females) among animals older than calves (computed from authors' tabulated data).

Murie (1951:275) and Anderson (1958) reported about three times as many cows as bulls among adult wapiti counted in winter in the Jackson Hole area of Wyoming. That area had a long history of overstocking with wapiti. The sexes were harvested in similar numbers. On the other hand, although only about one-third as many bulls as cows occurred on the National Elk Refuge during winter, males were in the majority among the known winter losses (Anderson, 1958). State-wide ear tag returns indicated that fewer bulls than cows reached old age (Anderson, 1958).

Miers (1962) tallied the sex of wapiti observed in three successive rutting seasons in an expanding population in the Stuart Mountains of New Zealand. Computed from his tabulated data, the sex ratio among wapiti older than calves was 71:100.

To equate the sex ratio of observed samples to that of the population

of which they are part, it is necessary to assume that differences in the behavior or distribution of males and females are not causing differences in the probability of observing them. Schwartz (undated) mentioned that the solitary tendencies and higher elevational distribution of bulls did reduce the probability of seeing males as opposed to females in the Olympic Peninsula. In the Canadian Rockies, Cowan (1950) noted the tendency of bulls and cows to segregate, many bulls occupying ranges at higher elevations both winter and summer. Even during the rut many bulls were separated from the cows at any one time. Cowan dealt with the sampling problem by extensive reconnaissances of different habitats at various times of the year. Murie (1951:275) remarked that some smaller feed grounds in Wyoming had a preponderance of bulls, and both he and Anderson (1958) acknowledged that some adult bulls wintered at scattered locations off the Jackson Hole feed grounds, at higher elevations. However, both writers considered the number of bulls missed to be too small to affect the sex ratio greatly.

Murie (1951:276) concluded, "On the whole, it appears to be fairly well established that among mature elk females greatly exceed males in numbers but the cause is hard to find."

The composition of samples of wapiti taken in "non-selective" slaughters in some of the National Parks of Western Canada suggested that the sex ratio remained about equal to at least 18 months of age, but that from 30 months of age males were in minority.

Murie (1951:132) reported that wapiti entering the rut, particularly the bulls, are fat, but that, while the cows continue to eat regularly during the rut, the bulls eat less than formerly, and those engaged in breeding can be expected to expend energy very rapidly. As a result the condition of the bulls at the start of the winter is poor, whereas the cows are still fairly fat. It is logical to speculate, on the basis of Murie's observations,

that if male and female adults were to lose condition at similar rates during the winter, the bulls would be the first to exhaust their energy reserves and as a result would be more prone to winter mortality.

According to Altmann (1960), during the rut the yearling male wapiti, unlike the female of the same age, is driven from his accustomed group and from his dam by the harem bull, and is subsequently threatened by any bull that he encounters. During the rut adult bulls compete intensely for harems, and defend them against other males through threat and occasional combat. Christian (1959) and Christian, Flyger, and Davis (1960) have presented evidence for other mammals that social pressures and intraspecific competition can, by stimulation of the pituitary-adrenocortical system, lead to lowered resistance to other debilitating agents in accordance with the general adaptation syndrome of Selye (1950).

These considerations led to the hypothesis that, as a result of the activities and social interactions of the rut, the males older than calves might be physiologically stressed to a degree that would predispose them to a higher mortality than occurs among females.

The present study was conducted to examine, from specimens collected in the wild, some of the physical and physiological factors affecting the welfare of wapiti to learn how they are phased with the seasons of the year, and how they affect animals of different sex and age. The factors studied were: tooth wear, growth, the reproductive cycle, fat reserves, parasitism, and adrenal activity. In addition, the population dynamics of wapiti in some of the National Parks in Western Canada were examined in the light of the results of the other aspects of the study.

STUDY AREAS

Data were collected from wapiti in Elk Island, Jasper, Banff, and Waterton Lakes National Parks in Alberta, and to a minor extent from Kootenay National Park in British Columbia, and the Ya Ha Tinda Ranch east of Banff Park. Hereafter the words national park will be omitted, the name Waterton Lakes, for example, will refer to the Park rather than the townsite within it or the lakes after which it was named. The locations of the five parks are shown in Fig. 1. In Fig. 2, Banff, Kootenay, and the Ya Ha Tinda Ranch are shown with the major drainages within them.

In the mountainous areas there are pronounced local variations in climate, and weather stations are few. The approximate mean annual total precipitation, and approximate mean daily temperatures for January, April, July, and October for each park are shown in Appendix 1. The values are based on the Atlas of Canada (Dept. Mines and Tech. Surveys, 1957) and each refers to the area within which most of the particular park is located.

Elk Island Park, with an area of approximately 75 square miles, lies on the Cooking Lake Moraine, which has an undulating to hilly, knob and kettle topography, podzolic soils (Bowser *et al.*, 1962), and is assigned by Rowe (1959) to the Mixedwood Section of the Boreal Forest Region. Most of the park supports a *Populus* association in which aspen poplar (*Populus tremuloides*) dominates in the drier sites, and balsam poplar (*Populus balsamifera*) in the more moist situations (Moss, 1955). Throughout the park are scattered grassy areas many of which, during the period 1959 to 1966, were being invaded by aspen poplar. Soper (1951) described the history of the park and its mammalian fauna. The wapiti are descendants of those native to the area when the park was established.

They share the park with four other ungulates: moose, white-tailed deer (*Odocoileus virginiana*), mule deer, and bison (*Bison bison*).

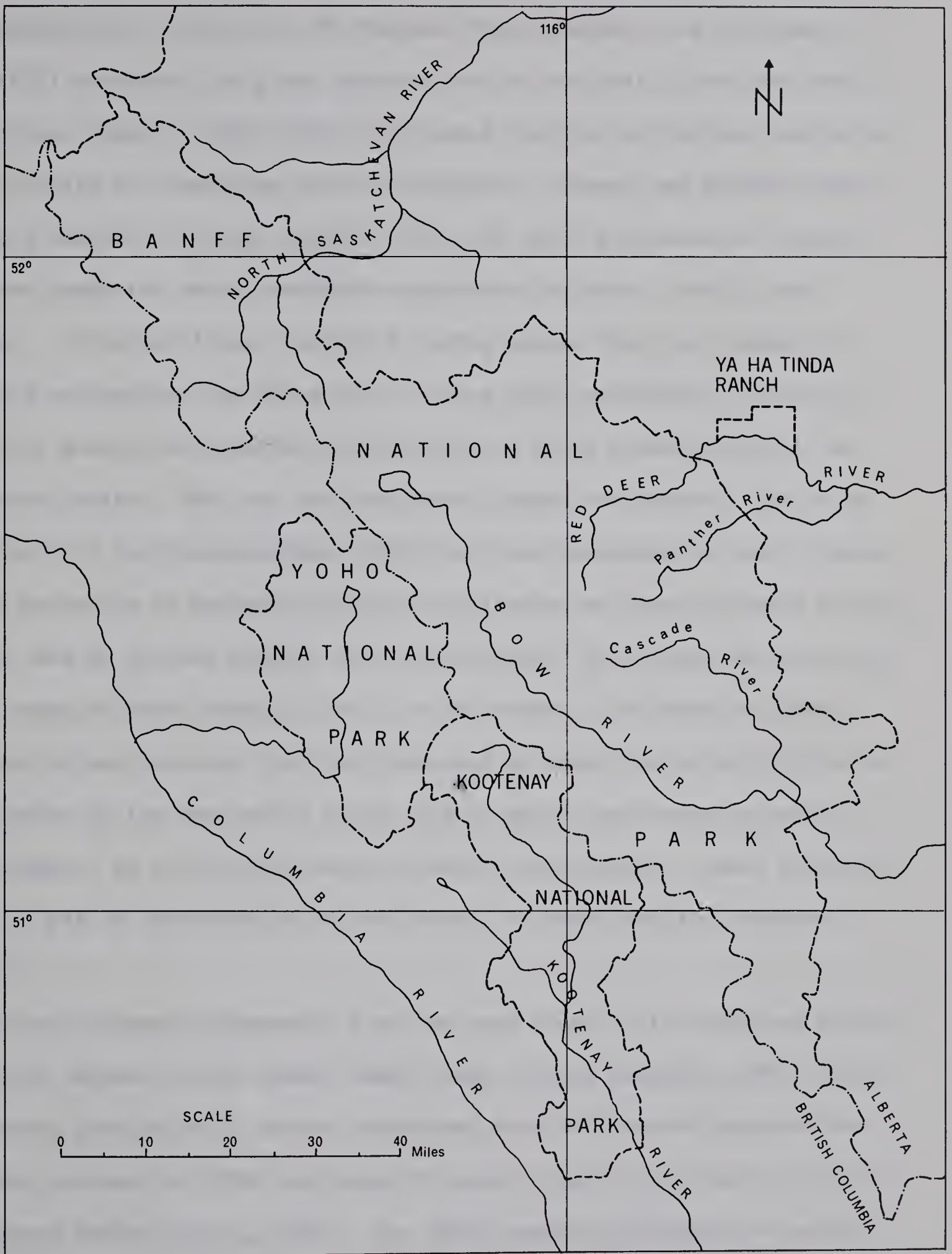
Estimates of numbers of wapiti, moose, and deer (species of deer not distinguished) in Elk Island from aerial surveys from 1959 to 1966 (Flook, 1960; Lovaas, 1961; Blood, 1962, 1964, 1966a) are given in Appendix 2. Numbers of wapiti and moose removed in slaughters are shown, and pre-slaughter estimates computed from the numbers slaughtered and post-slaughter counts. While slaughters and recruitment have caused pronounced fluctuations in populations of wapiti and moose, there have been no indications of any large die-offs in recent years. Deer pass in and out of the park under the fence; and the park wardens report that moose occasionally slide over the fence during the rut. However wapiti have never been reported to do either. The number of bison in the enclosure as shown by park wardens' counts in the winter feed lot has varied during the period 1959 to 1966 between approximately 400 and 700. During that period bison have received hay in the winter although the cervids have not.

Jasper, Banff, and Waterton Lakes all on the east slope of the Rocky Mountains have areas of approximately 4,200, 2,585, and 204 square miles respectively. Kootenay, lying on the west slope of the Rockies has an area of 543 square miles. The Ya Ha Tinda Ranch, east of Banff, with an area of approximately 19 square miles is crown land used by the Parks Service for grazing horses. The geology of the parks in the Canadian Rockies is described by MacKay (1952). The major areas of Jasper, Banff, and Kootenay are included by Rowe (1959) in the East Slopes Rockies Section of the Sub-alpine Forest Region. However, there are substantial areas of Alpine Tundra, and the lower portions of the Athabasca and Bow valleys in Jasper and Banff, respectively, are assigned to the Douglas Fir and Lodgepole Pine Section of the Montane Forest Region. The lower part of the Kootenay Valley is assigned

Fig. 1. Map showing location of National Parks in which study was conducted.



Fig. 2. Map of Banff, Kootenay, and Yoho National Parks and the Ya Ha Tinda Ranch, showing major drainages.



to the Southern Section of the Columbia Forest Region. Rowe assigns the area of Waterton Lakes to three categories: Alpine Tundra, Douglas Fir and Lodgepole Pine Section of the Montane Forest Region, and Grassland. Moss (1955) discussed the plant associations of the East Slope, and their successional stages. Flook (1964) discussed the role of various vegetation types in Banff and Jasper as ungulate habitats. Grassy and shrubby stages following removal of forest cover by fire and other disturbances, provide extensive range for wapiti and other ungulates in Jasper, Banff, and Kootenay. On valley floors and south facing slopes there are areas of grassland and sparse tree cover with a grass shrub understory. Those are relatively stable and apparently maintained in their present cover by an arid microclimate. They are the key winter ranges for wapiti. The Ya Ha Tinda Ranch is rolling grassland, which has been dominated by rough fescue *Festuca scabrella* in periods of high precipitation or less intensive grazing, or both, and by shorter grasses in other periods. It is used in winter by wapiti, many of which range in Banff in the summer. In Waterton Lakes, extensive climax prairies that are dominated by rough fescue with groves of aspen poplar in the more moist sites, are of major importance as wapiti winter range. In all of the mountain parks, the potential summer range for wapiti is far in excess of the winter range, in both area and carrying capacity.

Wapiti almost disappeared from the east slope of the Canadian Rockies about 1900 (Miller, 1916; Green, 1946; Cowan, 1947b; Banfield, 1950, 1958). The present population in Jasper originated from 83 from Yellowstone Park that were released in 1920, and about 35 native wapiti that had survived in the Brazeau Valley (Lloyd, 1927). The Banff population originated mainly from the release, in 1918, of 10 wapiti of mixed Manitoba and Wyoming ancestry

and 41 from Yellowstone, and in 1920 an additional 194 from Yellowstone (Lloyd, 1927). Native wapiti survived in the East Kootenay district in British Columbia and probably were the principle progenitors of the present population in Kootenay, and contributed to the population of Banff as well (Banfield, 1958). The Waterton Lakes area was reoccupied naturally beginning about 1920, presumably by wapiti from Montana (Banfield, 1950).

The results of recent counts of wapiti by park wardens in Jasper, Banff, and Waterton Lakes are tabulated in Appendices 3, 4, and 5. The counts are acknowledged to be subject to variations from year to year due to weather, distribution and behavior of the animals, and changes in personnel. Wapiti from Glacier National Park, U.S.A., and probably from Alberta and British Columbia, have entered Waterton Lakes Park in winter, the number varying, apparently in relation to snow depths. In the light of recent observations of movements of wapiti between winter ranges within Waterton Lakes, it is suspected that some of the higher counts in that park may have included duplications. All other counts in the mountain parks are believed to have been lower than the populations they represented. The apparent decline in the Bow Valley from 1963 to 1965 is thought to represent, in part at least, a real decline resulting from slaughters. Park wardens' counts of wapiti in Kootenay in November in the years 1962 to 1965 varied from about 350 to 480. The numbers declined as the winter advanced suggesting a movement down the Kootenay Valley and out of the park. In all parks, survival of calves is thought to have varied considerably from year to year depending on the severity of winter weather, but there has been no evidence of major die-offs during the period of the study.

It is pertinent to consider the importance of predators in the parks. Of the carnivores present, only wolves (*Canis lupus*), and cougars (*Felis concolor*) are thought to prey on ungulates to a sufficient extent to warrant

consideration as potentially important agents of mortality. Schwartz and Mitchell (1945) reported that cougars were preying upon wapiti in Washington, and Banfield (1958) mentioned predation on wapiti by a cougar in Banff.

No data are available to indicate whether either sex or any age group tends to be preyed upon more than others. Cougars, or their tracks, have been seen from time to time in all the mountain parks, but, probably, they have not been sufficiently abundant anywhere in the parks to have a significant influence on populations.

Cowan (1947a) estimated the wolf population of Jasper from 1942 to 1946 at between 33 and 50 individuals. Park wardens' reports of wildlife observations suggest that wolves were present in the park continuously from 1951 until the time of writing, although probably in smaller numbers than in the period of Cowan's study. Cowan (1947a) reported that after having been absent from Banff for some time, wolves entered the park in 1942-43. According to Green (1951), they increased from 1944 to reach a peak in 1947 estimated at 48 individuals. In 1952-53 their numbers were reduced by poisoning for rabies prevention (Banfield, 1958). Banfield (1958) estimated that there were 4 wolves in Banff in 1953 and 10 to 12 in 1956. Park wardens' reports of wildlife observations from 1956 until 1964 indicate that wolves were scarce in the park throughout that period, and that they were probably absent in 1961 and perhaps only visitors in some other years.

For many years wolves have been only rare visitors in Kootenay and Waterton Lakes Parks (Cowan, 1947a; Banfield, 1950; and park wardens' reports of wildlife observations).

Cowan (1947a) found that wapiti were the most important single food item of wolves in Jasper and Banff in 1943 to 1946. His comparisons of sex and age ratios of wapiti on wolf-inhabited and wolf-free areas indicated

that wolf predation had little or no effect on the composition of the wapiti population.

GENERAL METHODS

Data on various phases of the study were obtained from 1957 until 1967, from wapiti shot in slaughters conducted for population control in Elk Island, Banff, Waterton Lakes, and the Athabasca Valley of Jasper. Most collection of data was done by park wardens. In Banff and Jasper in 1966-67 and in Elk Island in several slaughters, other staff members of the Canadian Wildlife Service participated, and in the latter park zoology students from the University of Alberta also assisted. The writer participated in data collection in all the parks at different times, demonstrated techniques to new observers, and checked the accuracy of the data collected.

In order to obtain detailed data at different seasons of the year, 107 wapiti were autopsied from July 9, 1961 to October 15, 1962. Initially the plan was to collect two animals of each sex of each of two age-groups, yearlings, and animals 2 years old and older, at intervals of 4 to 6 weeks. In the first few months of collecting it became evident that 2-year-olds differed from older animals in a number of parameters, and it was found that 2-year-olds, particularly males, could be distinguished from older animals with fair success. In later collections, it was therefore attempted to include three age groups: yearlings, 2-year-olds, and animals 3 years old and older. Forty animals in this series were taken in the slaughter in 1961-62 in the Bow Valley, and the Cascade, Panther, and Red Deer drainages in Banff. Most of the remaining animals were shot in the last three mentioned drainages in Banff. At the times of year when wapiti of the appropriate sex and age were not readily available in those areas, animals were taken on the Ya Ha Tinda Ranch, in the Bow Valley, or in the Kootenay drainage. In addition one specimen was examined on the Ranch in

February, 1963, and eight were collected in Banff in the autumn and early winter of 1965, to study changes in the liver during the rut. The series of 116 specimens will be referred to hereafter as the research series.

There is thought to be little movement of wapiti between the Bow Valley and the Cascade, Panther, and Red Deer drainages. However, there are indications of movements among the last three areas. In the sections on parasites and population dynamics, samples from Banff and the Ya Ha Tinda Ranch will be designated as having come from either of two areas, one being the Bow Valley and the other being the Cascade and Red Deer drainages, the latter including the Panther Valley and the Ranch.

A small series of skulls and skins of wapiti collected from Elk Island, Banff, and Waterton Lakes during the study were deposited in the National Museum of Canada, Ottawa.

Specific methods for each phase of the study will be discussed in the section of the paper dealing with that phase. In statistical comparisons 0.05 was the probability level at which the null hypothesis was rejected. Only in tests in which the probability of a larger value of t , F , or χ^2 is equal to, or less than 0.01, will the probability be given.

TOOTH WEAR AND CEMENTAL DEPOSITION

The teeth were studied for two reasons. The amount of wear on the occlusal surfaces, and the numbers of cemental layers provide alternative criteria for estimating age. Also as deterioration of the teeth through wear could reduce the efficiency of food utilization it is a potentially important feature of senescence.

Dentary bones were collected from all wapiti taken during the period of the study. They were assigned to age classes by criteria based on tooth replacement and wear (Quimby and Gaab, 1957). Prior to December, 1960, wear patterns of the molariform teeth were compared with the illustrations and descriptions published by Quimby and Gaab (1957). In 1960, Quimby kindly selected from a collection of dentaries from Waterton Lakes, a series showing conditions comparable to those represented in his collection of specimens of known age. Specimens representing the conditions of each age class from calves to 9-year-olds and the inclusive groups, 10 - 15 years and 16 - 21 years comprised the series. The series, supplemented by Quimby and Gaab's (1957) published illustrations and descriptions, was used in assigning age to wapiti shot in all subsequent slaughters. Quimby and Gaab showed that variation in tooth wear limits the precision with which individual age can be established, particularly as age increases.

Beginning with the specimens slaughtered in the winter of 1961-62, wapiti 2 years old and older were also assigned ages by counting seasonal layers in the dental cement by the method devised by Mitchell (1963) for red deer (*Cervus elaphus*). A few yearling wapiti were included.

A lapidary saw was used to cut through the dentary between the cusps of the first molar, cutting through the thickest part of the cemental pad which lies between the roots (Fig. 3). Both surfaces exposed by the cut were

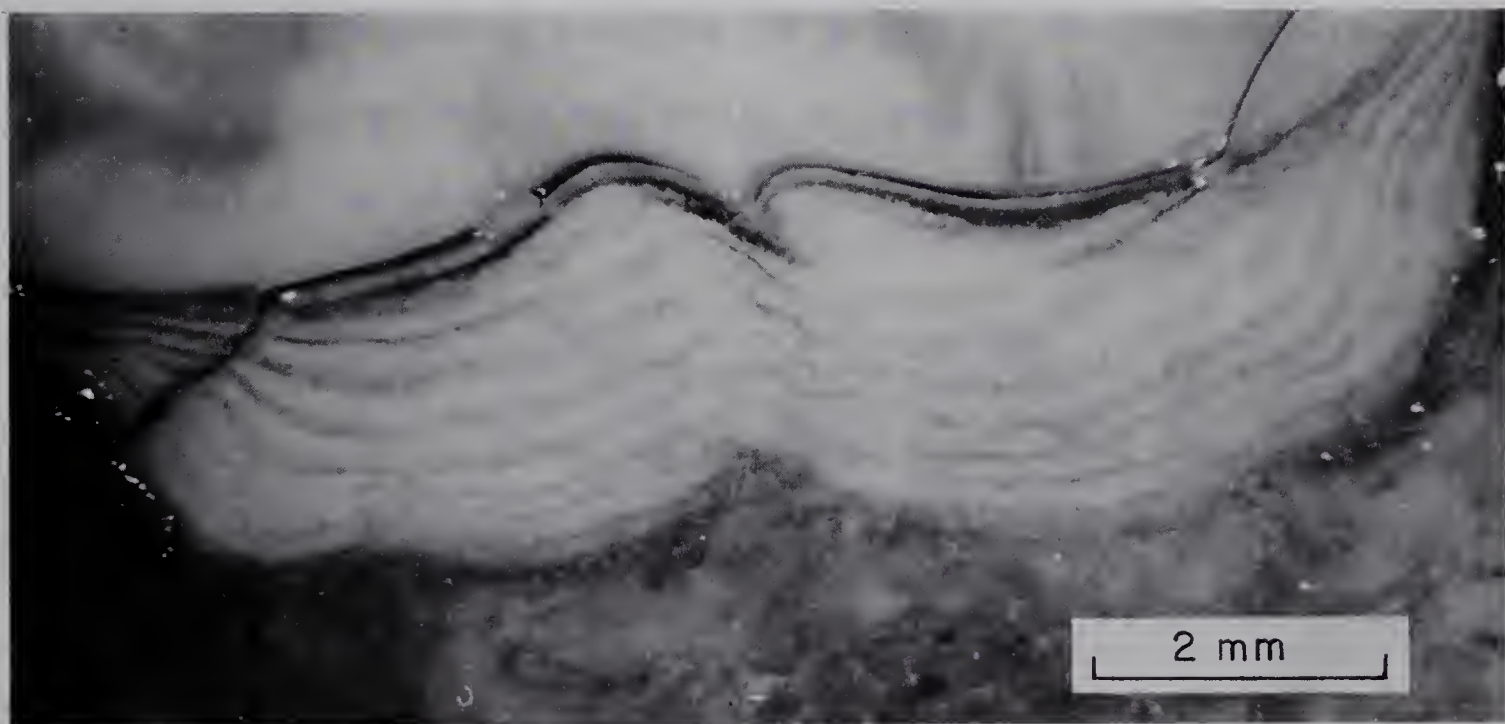
examined under direct light at 16X magnification, using a stereomicroscope. No polishing was necessary, but the exposed surfaces were usually covered with a film of alcohol or water to facilitate clear viewing of the cemental layers.

Mitchell (1963) sawed the first lower molar through the cemental pad between the roots and found alternating translucent and opaque layers of cement. He found that the opaque cement was associated with summer growth and the translucent cement with winter growth. A few red deer 21 months old had a thin layer of opaque cement followed by a translucent outermost layer. However, in most cases the first cement produced was a thin translucent layer deposited during the second winter of life, and that was followed by an opaque layer during the third summer. Mitchell counted 16 layers of opaque cement in the first lower molar of a red deer stag of a known age of 17 years 4 months. Low and Cowan (1963), and Ransom (1966) demonstrated that in known-age specimens of Columbian black-tailed deer (*Odocoileus hemionus*) and white-tailed deer, respectively, each pair of alternating major light and dark layers of cement could be equated to one year of life after the onset of cemental deposition.

Since the mandibles of yearling and 2-year-old wapiti can be assigned to age classes with certainty on the basis of tooth replacement (Quimby and Gaab, 1957), they were used to ascertain the age at which cemental production begins under the first lower molar. A thin layer of opaque cement was present in all yearlings killed in early winter; and a thin opaque layer, a thin translucent layer, and a second opaque layer, thicker than the first, were present in 2-year-olds killed in early winter. A very few specimens had, in addition, adjacent to the dentine, a trace of opaque cement followed by a trace of translucent cement, evidently deposited

Fig. 3. Method of cutting dentary and first molar with lapidary saw to expose cemental layers.

Fig. 4. Cemental layers exposed by cut between roots of first lower molar of female wapiti shot in Jasper National Park, January, 1967, at an estimated age of 9 years. Photomicrograph under direct light.



in the first year of life. Those deposits were so small in thickness and area that there was no likelihood of mistaking them for the cemental layers produced during the second year of life.

Of 14 specimens of various ages taken between September 15 and February 21, all appeared to have opaque cement adjacent to the periodontal membrane. Of eight specimens taken between March 29 and July 9, one taken May 28 showed a trace of opaque cement adjacent to the periodontal membrane, and the remaining seven appeared to have translucent cement adjacent to the membrane.

On the basis of the above observations, ages were assigned from cemental layers by assuming that the first layer of opaque cement was deposited early in the second year of life, and thereafter a translucent layer was deposited annually in late winter and spring, and an opaque layer, in late summer and autumn. The date of birth of all specimens was assumed to have been June 1, and each age assigned will refer to that of the previous birthday. The age in years, of a specimen taken in December, for example, was estimated by counting the number of translucent layers enclosed between opaque layers and adding one year. Fig. 4 shows the sectioned cemental pad of the first lower molar of a wapiti of an estimated age of 9 years.

Ages given for specimens taken prior to December 1, 1961 were assigned from tooth wear, and those given for specimens taken after that date were assigned from cemental layers. In comparing age assigned from the tooth wear to age assigned from cemental layers, the latter will be referred to as "actual age".

Complete permanent dentition is attained in wapiti at about 30 months of age (Quimby and Gaab, 1957). Thereafter, the enamel ridges which form the cutting edges of the molariform teeth become progressively abraded. The

linear amount of enamel cutting edge becomes reduced as the lateral convolutions and the infundibula are worn away, particularly in stages beyond Quimby and Gaab's 7-year-old class. One might expect that the wear of the teeth beyond a certain stage would reduce the efficiency with which the animal utilizes forage.

Assigning specimens to Quimby and Gaab's age classes provides an objective method of measuring the degree of tooth wear. In order to learn whether there were differences in the rate of wear of the teeth of wapiti populations in different habitats, and of males as compared to females, all specimens 2 years old and older that were taken after December 1, 1961 were assigned an age by visual comparison of the teeth to the series assigned to age classes by Quimby. Ages were then estimated by counting the cemental layers, with no reference to the age previously assigned from tooth wear.

Using the resulting data, linear regressions of age estimated from tooth wear, on age estimated from cemental layers, were calculated for wapiti of each sex from each of the four parks: Jasper, Banff, Waterton Lakes and Elk Island (Figs. 5 and 6). In samples from each park, specimens assigned to the broad categories 10 - 15 and 16 - 21 years old on the basis of tooth wear, were excluded from the regression analyses, along with those of equal or greater "actual age". All specimens are plotted on the graphs, but each regression line includes only the range of actual ages, which were used in the analysis.

Variations among the values of \hat{Y} at $X=2$, on the eight different regression lines, make the regression coefficients imperfect as measures of the rate of tooth wear. A more precise estimate of the mean rate of tooth wear of each sex in each park was calculated as follows:

[("tooth-wear-age" from regression at 10 years' actual age)-2] / 8.

Fig. 5. Linear regressions of age estimated from tooth wear on age estimated from cemental layers in wapiti of each sex from Jasper (above) and Banff (below) National Parks. Value beside each plotted point represents number of specimens.

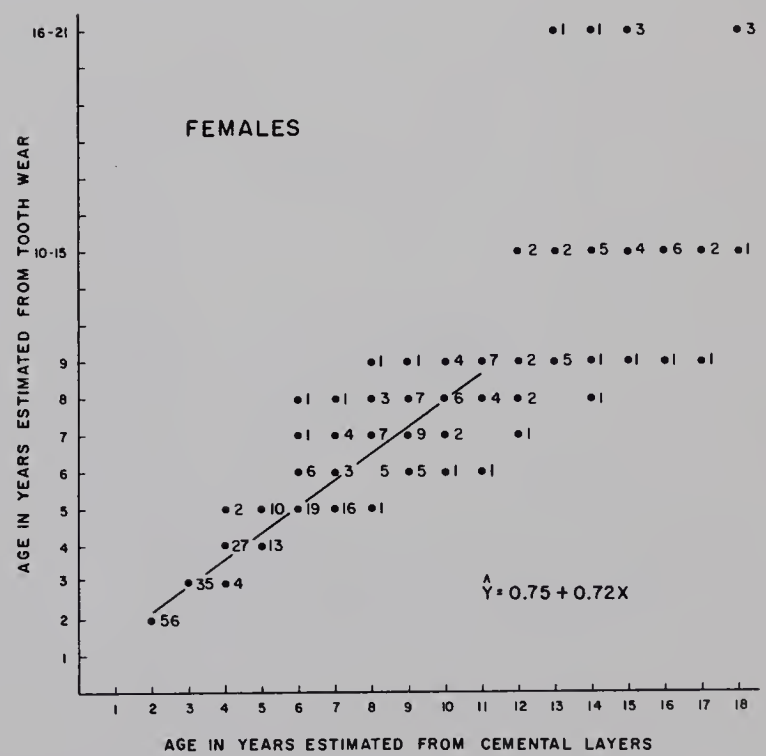
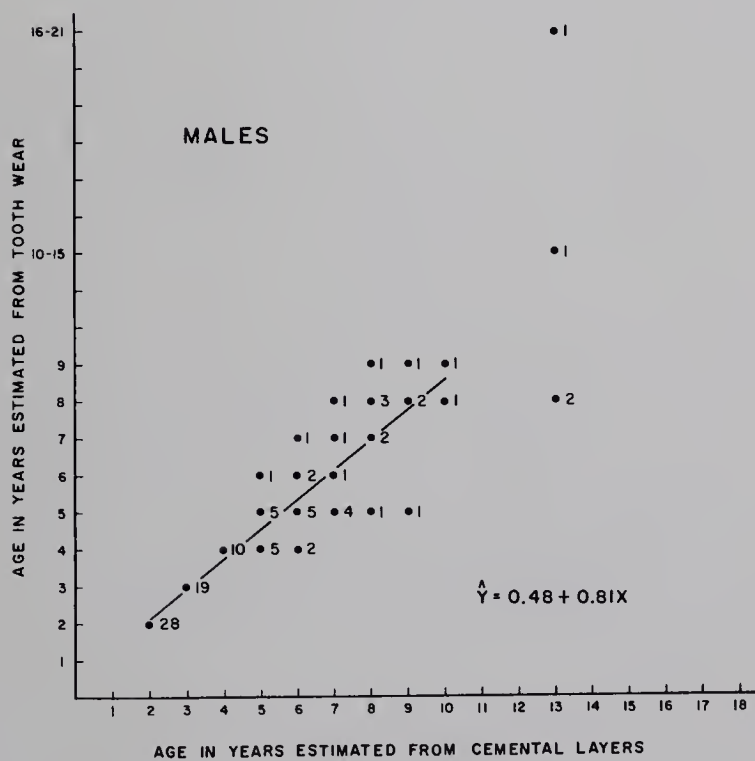
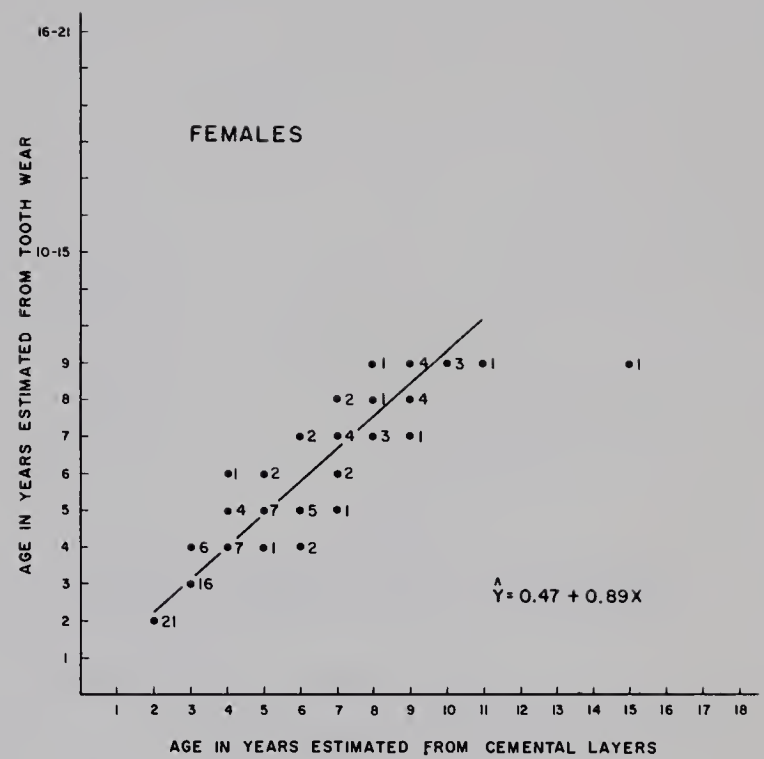
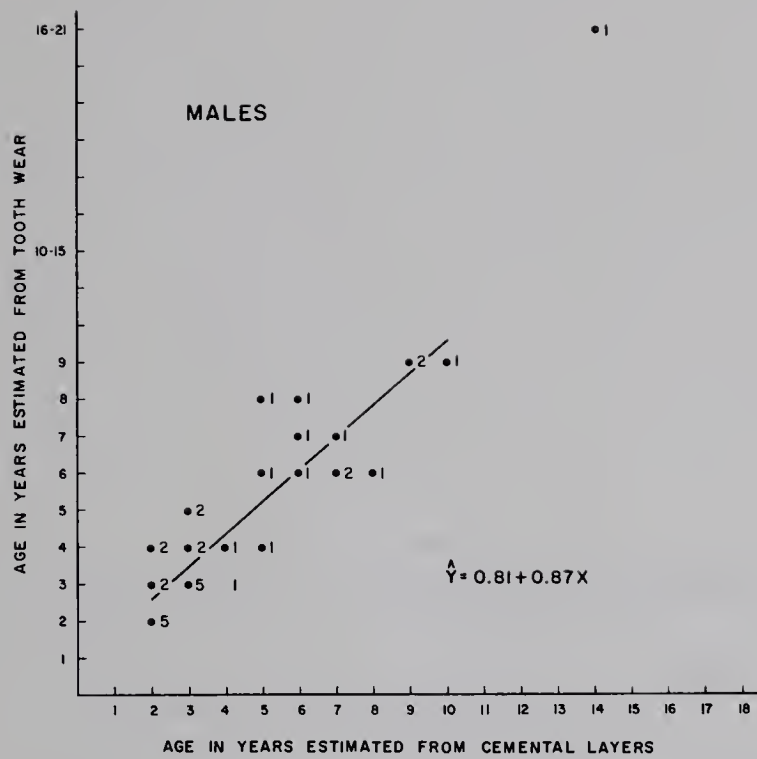
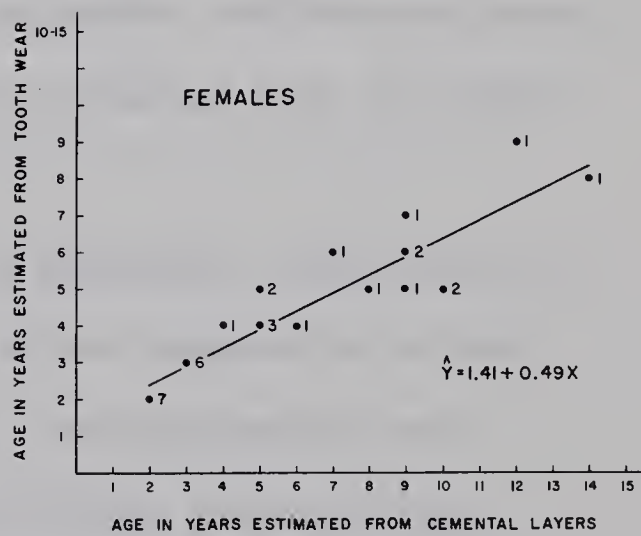
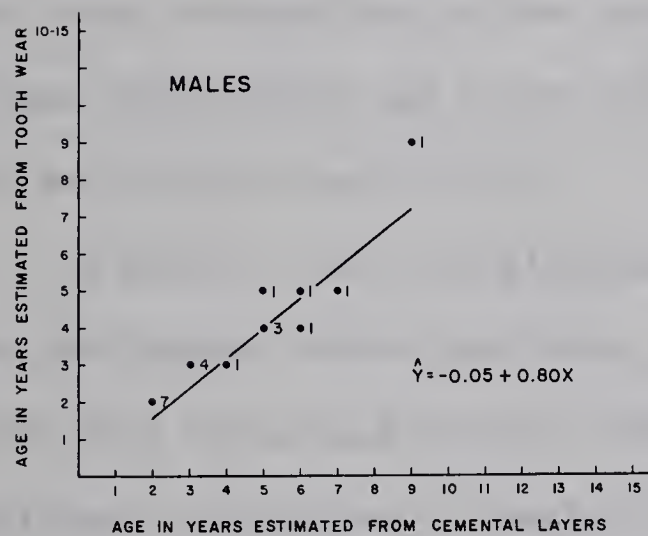
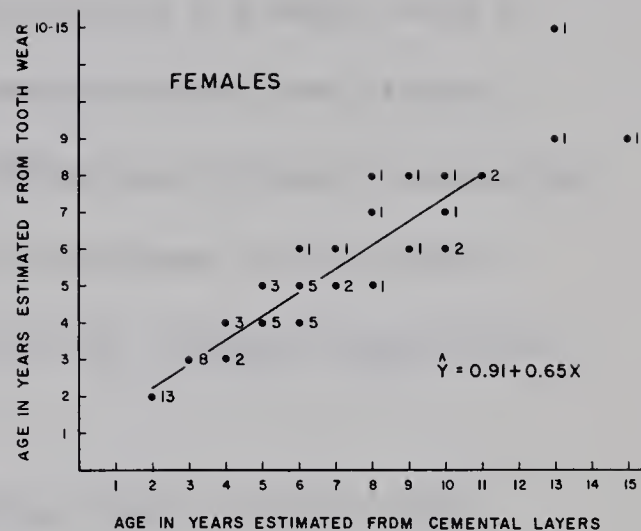
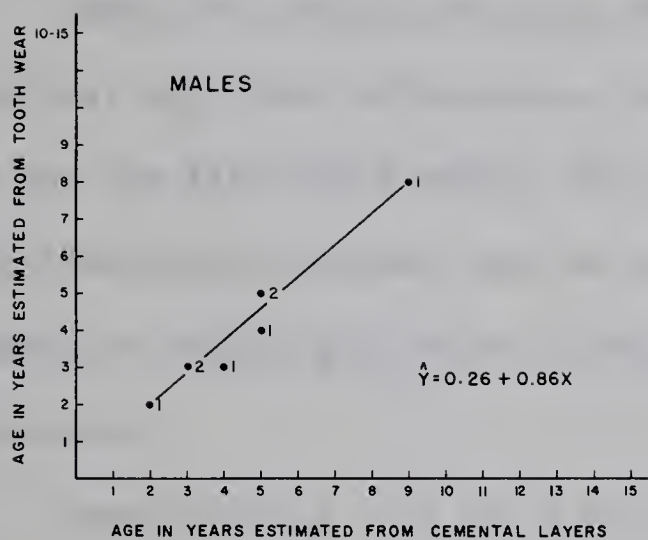


Fig. 6. Linear regression of age estimated from tooth wear on age estimated from cemental layers in wapiti of each sex from Waterton Lakes (above) and Elk Island (below) National Parks. Value beside each plotted point represents number of specimens.



The computed value represents the average amount of abrasion that occurs in one year of life. It is represented in units that correspond to the amount of abrasion between Quimby and Gaab's (1957) successive age classes.

Regression coefficients, mean rates of tooth wear calculated as described above, and actual ages corresponding on the regression line to 8 years' "tooth-wear-age" are represented in Table 1.

Among the samples of males from the four parks, the mean rates of tooth wear show some differences, the Jasper sample having the highest rate and the Elk Island sample the lowest. Differences between regression coefficients were smaller, and an analysis of covariance to test their homogeneity (Steel and Torrie, 1960:319-320) did not indicate significant differences.

Among females from the four parks the mean rates of tooth wear showed pronounced differences, the Jasper sample again having the highest rate, the Elk Island sample the lowest, and those from Banff and Waterton Lakes being intermediate in that order. The regression coefficients showed the same relationship and a test of homogeneity indicated that the differences were significant ($P < 0.01$).

In order to test for differences between regression coefficients of males and females within each park, an F value was computed by a homogeneity test (Steel and Torrie, 1960:173-174). The differences were significant in the case of samples from Banff ($P < 0.01$) and Elk Island ($P < 0.01$), but not significant in samples from Jasper and Waterton Lakes. The number of males available for study from Waterton Lakes was very small.

It is relevant that in a few specimens of either sex, the following sequence of layers was repeated through the cemental pad: a thick opaque layer, followed by a very thin translucent layer, a thin opaque or semi-

Table 1. Regression coefficients, mean rates of tooth wear, and actual ages corresponding on regression line to 8 years' "tooth-wear-age"

	Regression coefficient		Mean rate of tooth wear		Actual age at 8 years' "tooth-wear-age"	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Jasper	0.87	0.89	0.94	0.91	8.3	8.5
Banff	.81	.72	.82	.75	9.3	10.1
Waterton Lakes	.86	.65	.86	.68	9.0	10.9
Elk Island	.80	.49	.74	.53	10.1	13.4

opaque layer, and another thin translucent layer. In view of the seasonal sequence of events in the lives of wapiti it seems probable that the thick opaque layer was produced in summer, the first translucent layer during the rut, the thin opaque or semi-opaque layer, during the period between the rut and the onset of severe winter conditions, and the second translucent layer, during the late winter and spring. Low and Cowan (1963) and Ransom (1966) reported a similar condition in the teeth of some mule and white-tailed deer, respectively, and gave it the above interpretation. In the wapiti in which the condition described above was recognized, the secondary, opaque or semi-opaque layers were markedly thinner than the primary, or summer layers, and were excluded from the count in estimating age.

If each translucent cemental layer counted represented one winter of life after the first, then the differences in regression coefficients are attributable to differences in the rate of tooth wear. However, an alternative explanation is that the differences are due to the groups with the lower coefficients having had a higher frequency of extra-annual cemental layers which were inadvertently counted as annual layers. In order to test that possibility, samples from Jasper and Elk Island were re-examined. Those populations represented the two extremes, the regressions of males and females exhibiting no significant difference in Jasper, but the greatest difference in Elk Island. If, in Elk Island, translucent cemental layers counted as annual layers were produced more frequently by females than by males, we might expect the average interval between succeeding translucent layers to be proportionately thinner in females when compared to that of males.

For each specimen 3 years old and older from Elk Island and Jasper, the greatest thickness of the cemental pad was measured, using a dissecting

microscope at a magnification of 16X with a micrometer disc mounted in the ocular lens. The results of those measurements in relation to the age of the specimens are presented in Table 2. The Elk Island females do not exhibit a smaller mean interval between cemental layers when compared to males of the same population than do Jasper females when compared to males of that population. The data therefore do not support the hypothesis that the groups with the lower regression coefficients had a higher frequency of secondary cemental layers. The interpretation that the differences in regression coefficients represent differences in the rate of tooth wear is the more acceptable.

In attempting to explain the apparent differences in rates of tooth wear between males and females, it is pertinent to know whether males have a larger occlusal surface than females. In samples of mandibles of wapiti 4 to 9 years old from Elk Island and Banff Parks there were no significant differences between males and females as regards the length of molariform tooth rows and crown widths of molariform teeth (Table 3), each measurement having been taken at the widest point. That would indicate that in the permanent dentition there is no difference associated with sex, in the area of occlusal surface available for mastication. The relationship of the rate of tooth wear of males to that of females varied considerably between the populations of the four different parks (Table 1). That seems to indicate that in at least some of those parks males have tended to use foods of different abrasive qualities than females.

The following hypothesis, offered to explain the indicated differences in rate of tooth wear between the sexes and between populations, while it is consistent with the available information, is still largely speculative. In Elk Island where the habitats used by the sexes were most similar, and

Table 2. Average intervals between cemental layers counted
in wapiti from Jasper and Elk Island National Parks

	Number of specimens	Average age (yr)	Average no. cemental layers	Average interval between layers (mm)
Jasper				
Males	23	5.1	4.1	0.51
Females	80	6.0	5.0	0.42
Elk Island				
Males	11	5.3	4.3	0.46
Females	23	7.0	6.0	0.44

Table 3. Measurements of mandibular molariform tooth row of adult wapiti

	Males (16)			Females (34)		
	Mean	Range	Standard error	Mean	Range	Standard error
Length of tooth row (mm)	139.9	131-148	1.11	138.9	129-148	0.60
Crown width of P3* (mm)	12.44	11.2-14.0	.152	12.29	11.0-13.8	.103
Crown width of M2* (mm)	17.78	16.9-19.2	.202	17.55	16.0-19.5	.166

*Nomenclature follows that of Riney (1951)

presumably therefore the forage used was also most similar, the difference in rate of tooth wear between the sexes was the greatest among the populations studied. As data indicated that the occlusal surfaces of males and females are of equal area, it is suggested that the more rapid rate of tooth wear of males was caused by a greater annual food intake.

It is hypothesized that differences in the ranges used by wapiti in the four parks lead to the differences in tooth wear between populations. It is suggested that a sex difference in annual intake of forage is common to wapiti in all the parks, but that in the mountain parks its effect on tooth wear is compensated to various degrees by differences in the distribution of the sexes and associated differences in the amounts of abrasive material eaten in or with their forage.

Grasses are the major component of the diet of wapiti in some areas (e.g. Cowan, 1947a). They are characteristically high in silica (Bonner and Galston, 1952:69), most of which is in the form of opaline phytoliths (Baker, Jones, and Wardrop, 1959). Healy and Ludwig (1965) found the content of opaline phytoliths in pasture grasses about ten times as high as that in clover. Baker *et al.* (1959) found that the hardness of opaline phytoliths exceeds that of the enamel of sheep's teeth. They considered the consumption of phytoliths in forage an important factor contributing to the wear of sheep's teeth in Australia.

Severinghaus and Cheatum (1956:94) found that the rate of tooth wear in white-tailed deer was approximately doubled in specimens foraging in areas where the vegetation carried quantities of abrasive material on the surface.

Healy and Ludwig (1965) showed a direct relationship between the degree of wear of sheep's incisors on three New Zealand farms, and the

amount of soil consumed. They demonstrated the abrasive qualities of the soil experimentally and concluded that differences in soil consumption were the cause of the observed differences in tooth wear. As the average incisor height of 5-year-old ewes on a high-wear farm was less than one third that of ewes of the same age on a low-wear farm, the contrast appears to have been greater than that observed between the populations of wapiti in the present study. The consumption of phytoliths varied little between farms. They made up only about one tenth of the abrasive material consumed on the high-wear farm but most of the abrasive material consumed on the low-wear farm. Thus, where tooth wear is light, differences in the consumption of either phytoliths, or extraneous sediment, or both, could be important in causing differences in rate of wear in herbivores. There are reasons to expect variations in the consumption of silica from both of those sources among the populations of wapiti studied.

At low and medium elevations there appears to be a gradient in certain characteristics of the ranges from Jasper to Banff, Waterton Lakes, and Elk Island, in that order, the same sequence as the decreasing trend in rate of tooth wear. In the Athabasca Valley in Jasper, the grasses are shortest and sparsest, the soil most sandy, and the preferred forbs and browse plants the most scarce of the ranges of wapiti populations studied. Sediment from glaciers that feed the Athabasca River is deposited by the river where it passes through the major winter ranges. Winds frequently pick up sediment from the beaches and dunes along the river and other areas where plant cover is sparse and deposit it over the grassy areas. In contrast to Jasper, blowing sediment is negligible on ranges in the other parks. In Banff, grass stands have a higher proportion of tall species, and are more dense, and browse is somewhat more abundant than in

Jasper. Stands of grass in Waterton Lakes are much taller, and fairly dense, and browse and forbs are fairly abundant. In Elk Island, grass stands are of moderate height and fairly dense, but limited in extent, and browse and forbs are abundant.

Data on food habits from the various parks indicate a close relationship between the relative abundance of grass, forbs, and browse, and their proportions in the diet of wapiti. Cowan (1947a) showed that the winter diet in the Athabasca Valley was almost exclusively grasses. Preliminary data from Banff (Flook, unpub) indicate that grasses and sedges are the major component of the diet at most times of the year, but use of forbs in summer, and browse in summer and winter is substantial. Holsworth (1960) showed that in Elk Island, browse comprised most of the winter diet, and browse and forbs together made up most of the summer diet.

Wapiti using browse, tall grasses, and forbs would be expected to consume less extraneous sediment than those using short grasses, particularly where the latter are sparse and soil is exposed. Also a higher proportion of forbs and browse in the diet could be expected to be accompanied by a lower consumption of opaline phytoliths.

Males tend to spend more of their lives at higher elevations than do females (Cowan, 1950, and data to follow). The writer suggests therefore that males in the mountain parks tend to use more forbs and browse than do females, those plants being more abundant at higher elevations, and perhaps feed less on closely-cropped grass stands, and that therefore their diets contain lower proportions of abrasive material. That would be particularly so in Jasper where the areas farther from the Athabasca River would be less affected by blowing sediment.

Other factors being equal, animals that wear their teeth more rapidly can be expected to suffer the effects of inefficient food utilization at a younger age. In Quimby and Gaab's (1957) age classes the 8-year-old class shows particularly marked reduction in enamel ridges as compared to the younger classes. Apparently in Banff, males reached that stage of tooth wear on the average almost one year earlier than females (Table 1). In Waterton Lakes, the indicated sex difference is almost 2 years, and in Elk Island more than 3 years. It will be shown in the discussion that deterioration of the teeth is relevant to the question of longevity of the sexes.

BODY GROWTH

Little information concerning growth in wapiti is available from the literature.

Johnson (1951) reported a mean body weight of 32.5 lb (14.7 kg) and a mean hind foot length of 15.46 in. (39.3 cm) in a sample of 23 wapiti calves measured in their first day of life in Montana. The mean weight of males was heavier than that of females by 4.41 lb (2.0 kg).

Blood and Lovaas (1966) summarized data published by a number of authors on weights of entire and dressed carcasses of wapiti, as well as data on animals which they had weighed in Riding Mountain National Park, Manitoba. In each study the number of animals weighed in one area at one season of the year was small, and only the data collected by Blood and Lovaas (1966) included specific ages of all specimens.

Greer and Howe (1964) presented weight measurements of eviscerated carcasses of 271 male and 856 female wapiti of 5 age groups: calves, yearlings, 2-year-olds, 3-7-year-olds, and 8-year-olds-and-older, slaughtered in winter in Yellowstone National Park. They concluded, "A levelling off in weight [of males] appears to occur between the 3-thru-7-year group and the 8-year-and-older group but the data do not permit a reliable estimate for the age of maximum weight", and, "Females classified in the 3-thru-7-year group appear to have reached a maximum weight."

In the slaughters held in Banff in 1960-61, 1961-62, and 1962-63, entire carcasses were weighed to the nearest pound with viscera and antlers intact. Prior to weighing, all animals were bled by cutting the throat, but the weight lost in bleeding was variable because some animals bled internally more than others. Antlers were later sawn off, and weighed to the nearest 0.05 lb, and their weights subtracted from the total weight

to give body weight. Both body and antler weights were converted to metric units.

Chest girths and hind foot lengths were also measured. Bandy *et al.* (1956) pointed out that chest girth provides an indication of the bulk of an animal and relates closely to body weight, whereas hind foot length is a measure of skeletal size and is unchangeable once it has reached its maximum. Measurements were taken to the nearest one-quarter inch using a steel tape and were later converted to millimeters. Chest girth was measured immediately posterior to the axilla. The hind foot was measured from the proximal end of the calcaneum to the tip of the hoof, with the hock joint flexed enough to locate the proximal end of the calcaneum but not so much as to cause flexing of the toes.

Measurements of hind foot length, chest girth, and body weight are summarized in Figs. 7 to 9. Among the 73 males and 198 females 3 years old and older, on which data are included, 25 males and 84 females were taken in the 1960-61 slaughter, and their ages were assigned from tooth wear. The remaining 58 males and 114 females were taken during the two subsequent slaughters, and their ages were determined from cemental layers.

For each measurement it is useful to learn the age at which growth ceased and whether there was a reduction in size following the attainment of maximum size. Therefore, each graph was inspected and accumulative means and accumulative sums of squares were determined for the groups of age classes which appeared homogeneous and of adult size. That group was then compared with younger and older age classes or groups of age classes by analyses of variance. If the difference between the selected group of age classes of maximum size and the next youngest age class was

Fig. 7. Hind foot length of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.

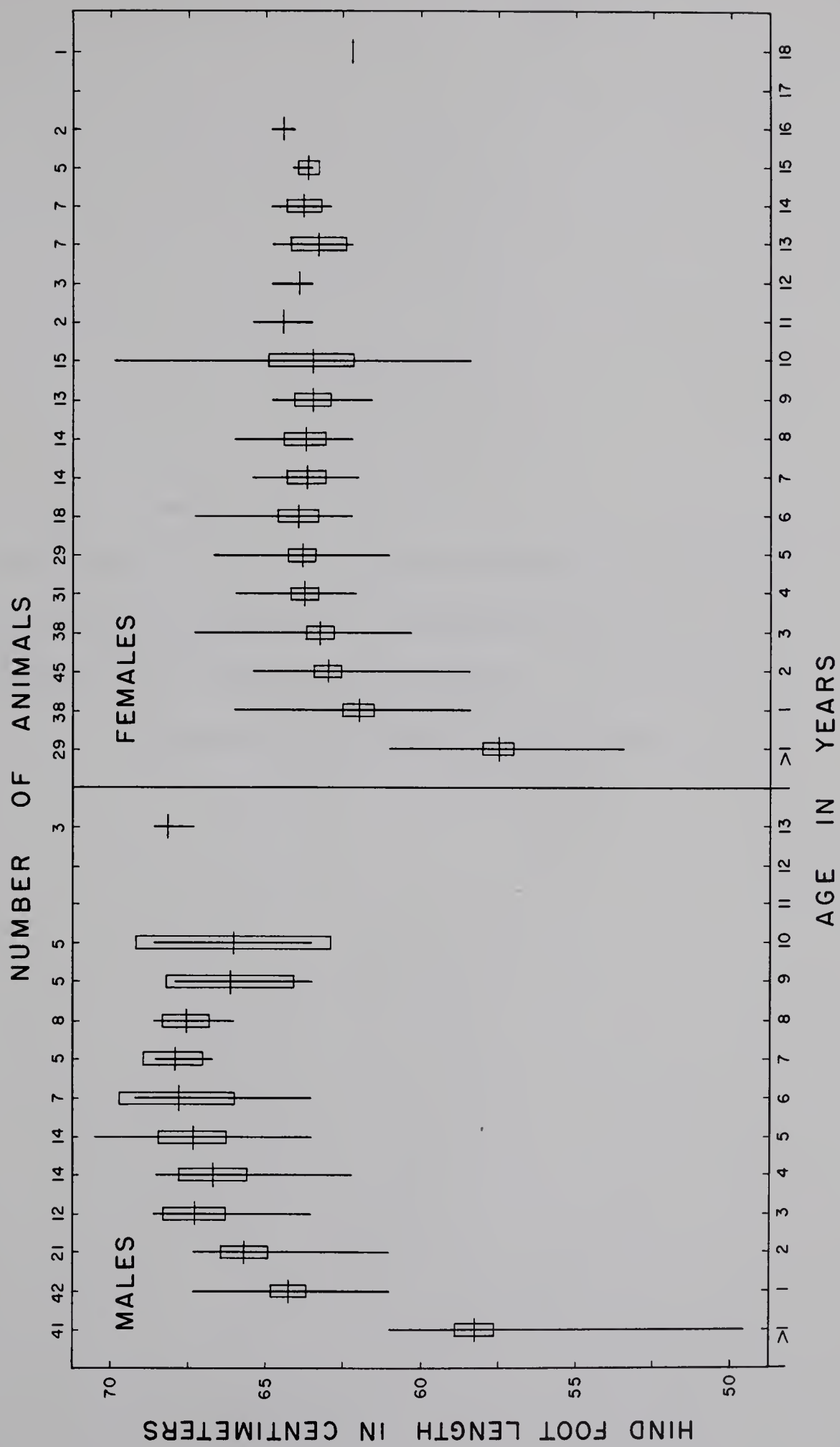
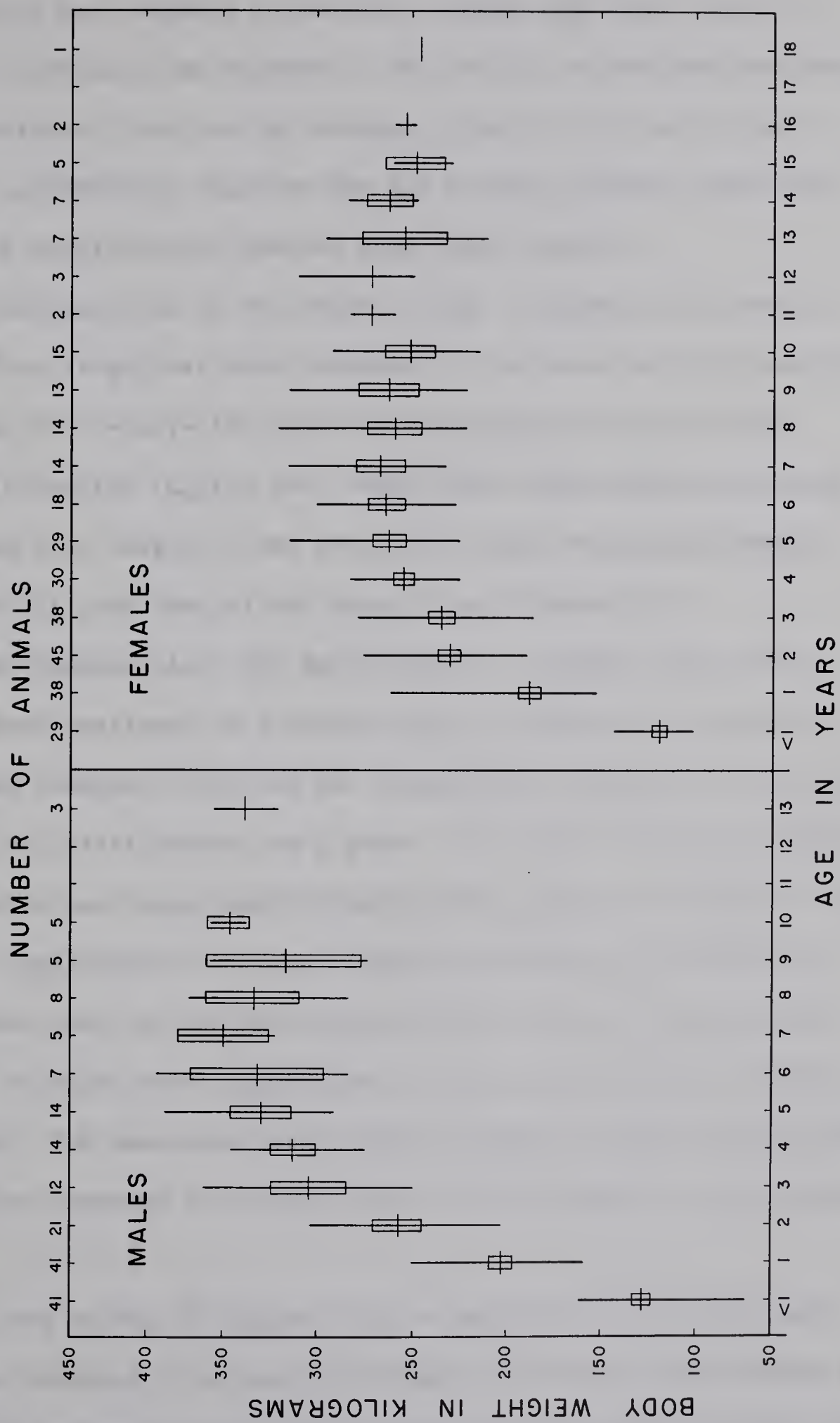


Fig. 8. Chest girth of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.

Fig. 9. Body weight of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.



not significant, then the latter was grouped with the former and the resulting group was compared to the next younger age class, until a significant difference was detected. The results of the analyses were considered evidence that, on the average, growth in the particular measurement continued at least to the age of the youngest class which was found not significantly smaller than older classes.

The configuration of the graph in Fig. 7 suggests that among males hind foot length may have continued to increase until 6 years of age. However the 3-year-old class was the youngest which was not significantly smaller in hind foot length than older males as a group. The mean hind foot length of the 2-year-old class was significantly smaller ($P < 0.01$) than that of the group 3 to 13 years old.

In the females also, the data in Fig. 7 suggest that slight growth may have continued to 6 years of age. However, the 4-year-old class was the youngest which was not significantly smaller in hind foot length than all older females as a group. The mean hind foot length of the 3-year-olds was significantly smaller than that of the group 4 to 18 years old. Inspection of the mean hind foot lengths and confidence limits reveals that for all ages represented by four or more animals, mean values of males were significantly greater than those of females of the same age. The mean hind foot length of males 3 years old and older was 67.3 cm as compared to a mean of 63.7 cm for females 4 years old and older.

The data in Fig. 8 suggest that in males chest girth may have continued to increase to an age of 10 years. However, the 5-year-old class was the youngest which was not significantly smaller in chest girth than all older animals as a group. The mean chest girth of 4-year-old

males was significantly smaller ($P < 0.01$) than that of the group 5 to 13 years old.

Among females the mean chest girth values of different age classes suggest a decline with advancing age after 10 years of age. The mean chest girth of females 11 to 18 years old was significantly smaller than that of the group 4 to 10 years old. The configuration of the graph suggests that in females maximum chest girth was not reached until 7 years of age. However, the 4-year-old class was the youngest which was not significantly smaller in mean chest girth than those older in the group 4 to 10 years old. The 2-year-olds and the 3-year-olds were not significantly different in chest girth from each other. However, both individually and grouped together they were significantly smaller ($P < 0.01$) in mean chest girth than the group 4 to 10 years old.

The confidence limits for mean chest girth of calves show no significant difference between males and females. However for all other age classes represented by four or more animals, mean values of males were significantly greater than those of females of the same age. The mean chest girth of all males 5 years old and older was 163.9 cm as compared to a mean of 149.2 cm for females 4 years old and older.

Mean body weights of males (Fig. 9) suggest that body weight continued to increase to a maximum at 7 years of age and then declined to a lower level which prevailed through the remainder of life. However none of the differences in body weight among age classes from 5 to 13 years of age were significant. Mean body weights of 3-year-old and 4-year-old classes were not significantly different from each other. However, both individually and together they were significantly smaller than the mean of the group 5 to 13 years old.

Among females the graph suggests that body weight continued to increase to an age of 7 years and decreased with advancing age after 9 years old. However the difference between the mean body weight of the group 10 to 18 years old and that of the group 5 to 9 years old was not significant. The 4-year-old class was the youngest which was not significantly smaller in body weight than all older animals as a group. The mean body weights of the 2 and 3-year-old classes were not significantly different from each other. However both individually and grouped together the body weights of those classes were significantly smaller ($P < 0.01$) than the mean of the group 4 to 18 years old.

Inspection of the mean body weights and confidence limits shows that for all age classes represented by four or more animals, males were significantly heavier than females. The mean body weight of all males 5 years old and older was 333 kg as compared to a mean of 259 kg for females 4 years old and older.

The data indicate that in males an increase in hind foot length continued to at least 3 years of age, and that an increase in chest girth and body weight continued to 5 years old. The graphs suggest that slight growth might have continued to 6 years in the case of hind foot length, 10 years in the case of chest girth, and 7 years in the case of body weight. If the chest girth really continued to increase beyond 7 years old while body weight failed to do so, the explanation is not known.

For females, the data indicate that growth as shown by each measurement continued to at least 4 years of age. However, the graphs suggest that slight growth might have continued to 6 years old in the case of hind foot length, and 7 years old in the case of both chest girth and body weight.

The graphs suggest a decline in hind foot length, chest girth, and body weight of males after 7 years of age. Among females the data suggest a decline in chest girth after 10 years of age and perhaps in body weight after 9 years of age. However the samples of old wapiti are small and variable. Only in the case of chest girth of females was the reduction statistically significant. Huxley (1931) reported that the body weight of red deer stags in an English park reached a maximum at about 10 years of age, after which it declined.

The early attainment of maximum hind foot length is consistent with the findings of Palsson and Verges (1952) with regard to lambs, that skeletal growth tended to occur earlier at the extremities and progress towards the central region of the body, and that bone had priority in growth over muscle and fat.

With reference to the observation that female wapiti attained adult body weight at a younger age than males, Wood, Cowan, and Nordan (1962) reported the same relationship in various races of deer of the species *Odocoileus hemionus*. Similarly, a growth curve for European moose (*Alces alces*) published by Skuncke (1949) and reproduced by Peterson (1955:77) indicated that on the average the maximum body weight in males was attained at about 12 years of age, whereas that of females with calves was reached at about 9 years. Skuncke's data showed a male superiority in body weight in moose, similar to that observed in wapiti in the present study, although his data did not show a difference in the weight of the sexes before 18 months old. Johnson's (1951) data indicated a male superiority in average body weight of wapiti at birth, and the present data show that among wapiti about 6 months old, males were significantly larger than females in both hind foot length and body weight.

Data presented later show that female wapiti taken during the slaughters had fat deposits that were, on the average, at least equal to those of females taken at any other time of year. The fat reserves of males taken during the slaughters were, however, smaller than those of females taken in the same period, and data collected throughout the year suggested that they had declined from a peak in August. We might therefore expect that the difference in body weight between males and females in similar physical condition would be greater than that observed in the sample taken in the slaughters.

REPRODUCTIVE CHARACTERISTICS OF THE MALE

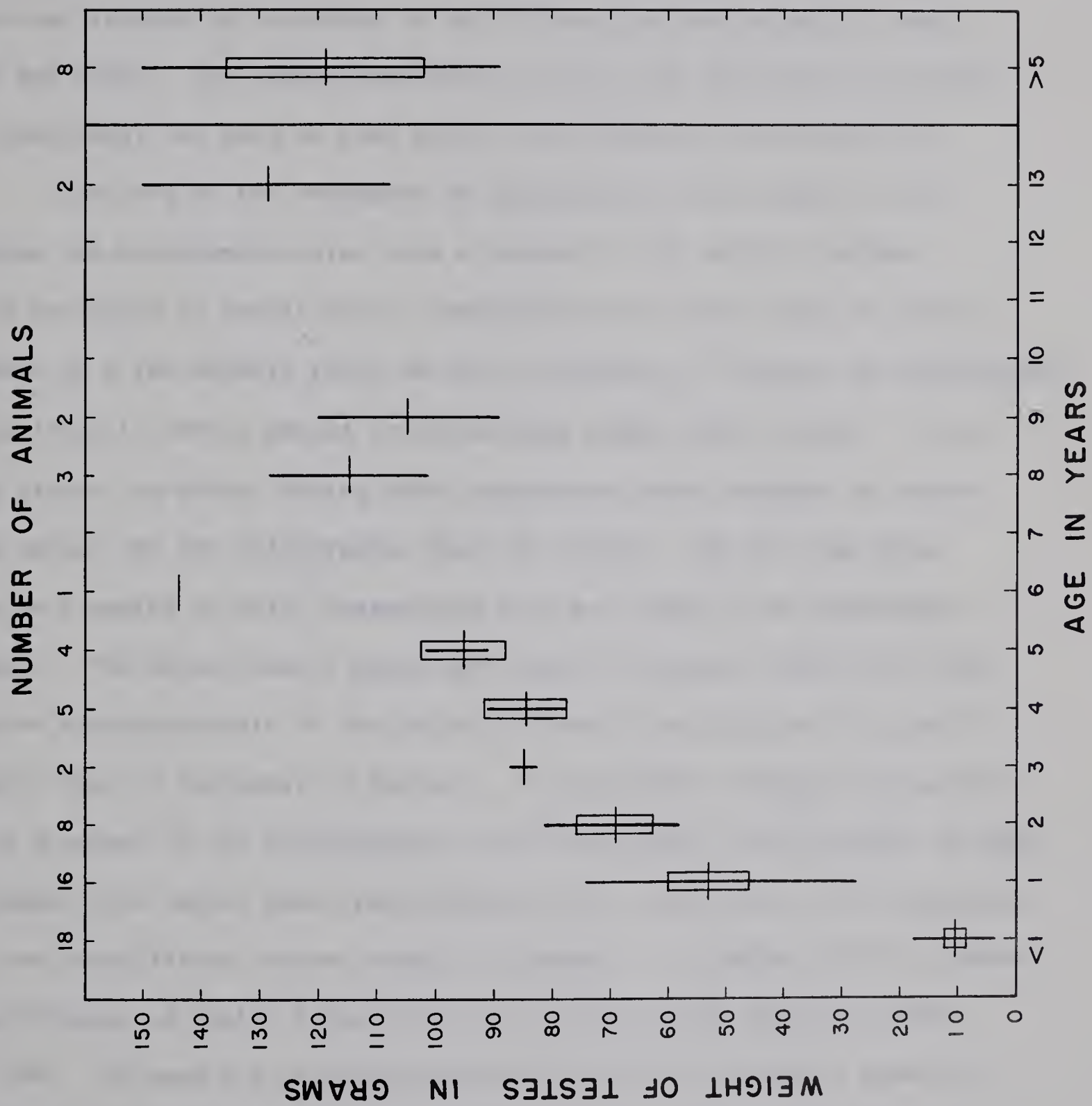
Testicular Changes with Season and Age

Testes were collected from all males slaughtered in 1961-62 in Banff, and from those in the research series. The epididymides were removed and the testes weighed to the nearest gram.

The weights of testes of the males taken in the slaughter are summarized in relation to age in Fig. 10. The values represent the sum of the weights of the right and left testes. The data indicate an increase in testis size each year from the calf class to at least 6 years old and probably older. The mean weight of testes of the 5-year-old class was significantly smaller than that of the group 6 to 13 years old. Among specimens older than 5 years, weight of testes did not vary significantly in relation to age. However, data to follow indicate that testis size attains a peak in August and September from which it has decreased markedly by November. It is quite possible that among animals older than 5 years, there are differences in the maximum testis size attained during the peak of the breeding season that are associated with age.

One testis from each male in the research series was sliced transversely through the middle and the exposed surface smeared across a microscope slide. A smear was also prepared from the tail of the epididymis in the same way. The smears were dried in sunlight or near a gasoline lantern and stored. Later, without staining, each smear was scanned under a binocular microscope at 150 X and assigned to one of the following categories based on the absence or presence and abundance of spermatozoa: (0) no spermatozoa observed, (1) one to ten spermatozoa observed, (2) more than ten spermatozoa observed but not common, (3)

Fig. 10. Weight of testes of wapiti of each age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.



spermatozoa abundant but not packed together, (4) field packed with spermatozoa. The testes weights and spermatozoa abundance values are presented by month according to age group in Figs. 11 and 12.

A seasonal cycle in testis size is apparent. The peak of testis size was reached in September in both 2-year-olds and animals 3 years old and older. The autumn increase in testis size was much less marked in yearlings, but data on that group also conform to an autumn peak.

The data on the abundance of spermatozoa in the smears of the testes and epididymides also show a seasonal cycle which coincides with the cycle in testis size. Spermatozoa were first found in testis smears of a few animals taken as late as February. However, no spermatozoa were found in testis smears from yearlings taken after October. In all age groups the period during which spermatozoa were abundant in smears was longer for the epididymides than the testes. May and June were the only months in which spermatozoa were not found in any epididymal smears. The above results agree with those of Conaway (1952) who found active spermatogenesis in the testes of several yearling and one adult wapiti shot in September in Montana. He found that although spermatozoa were abundant in the epididymides of most specimens from September through December (the latest month represented in his collection), the regression of the seminiferous tubules began in November. Struhsaker (1967) studied the behavior of wapiti during the rut, in the Cascade Valley in Banff in 1965. He used the term heterosexual behavior to include a number of clearly defined behavioral interactions between males and females, and observed that the peak of such behavior was from September 8 to September 21.

Although Graf (1955) reported having observed a yearling male wapiti

Fig. 11. Abundance of spermatozoa in smears of testis and epididymus, and weight of testes, of individual yearling and 2-year-old wapiti, according to month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch. Each number beside plotted symbol represents number of specimens if in excess of one.

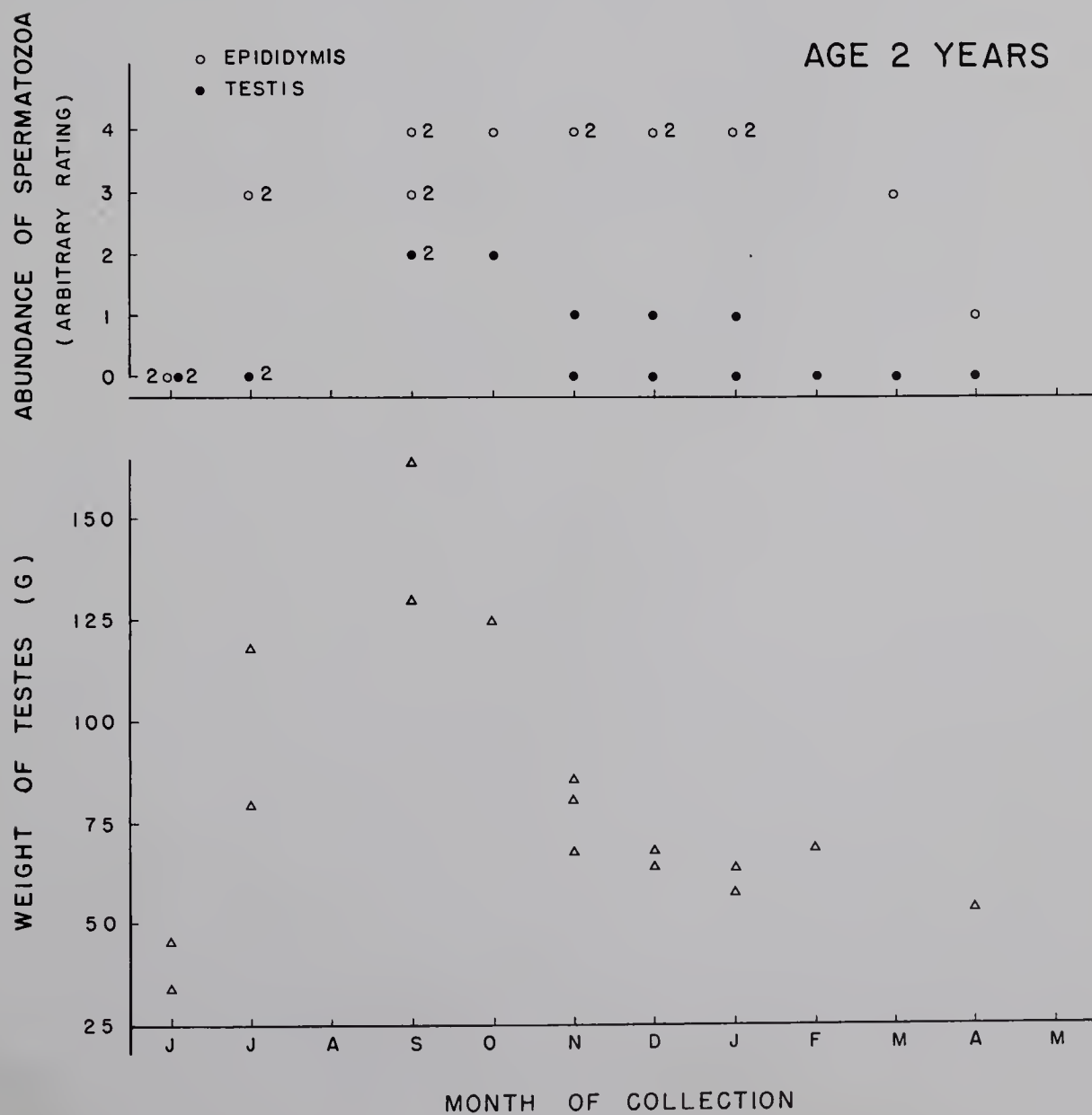
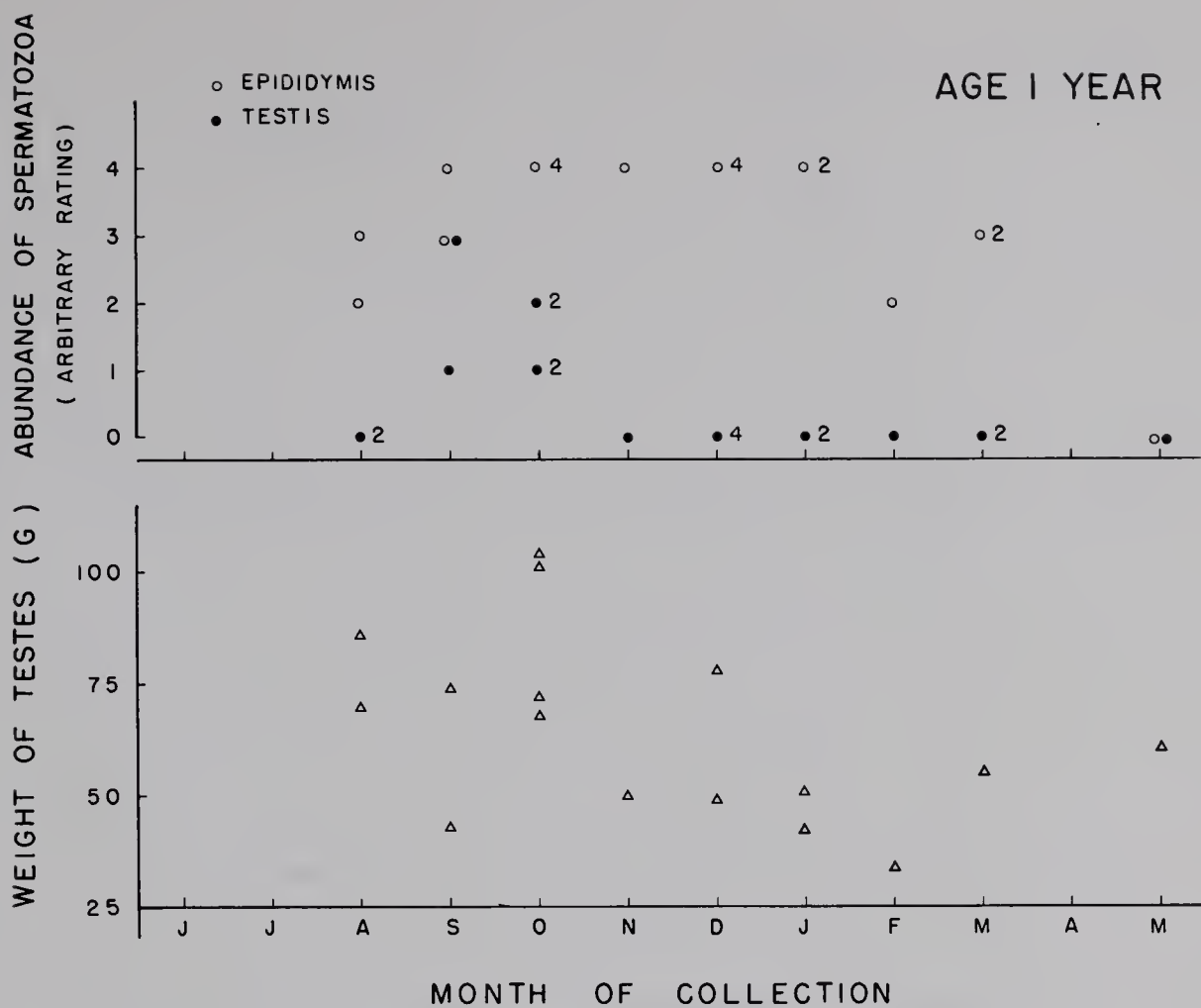
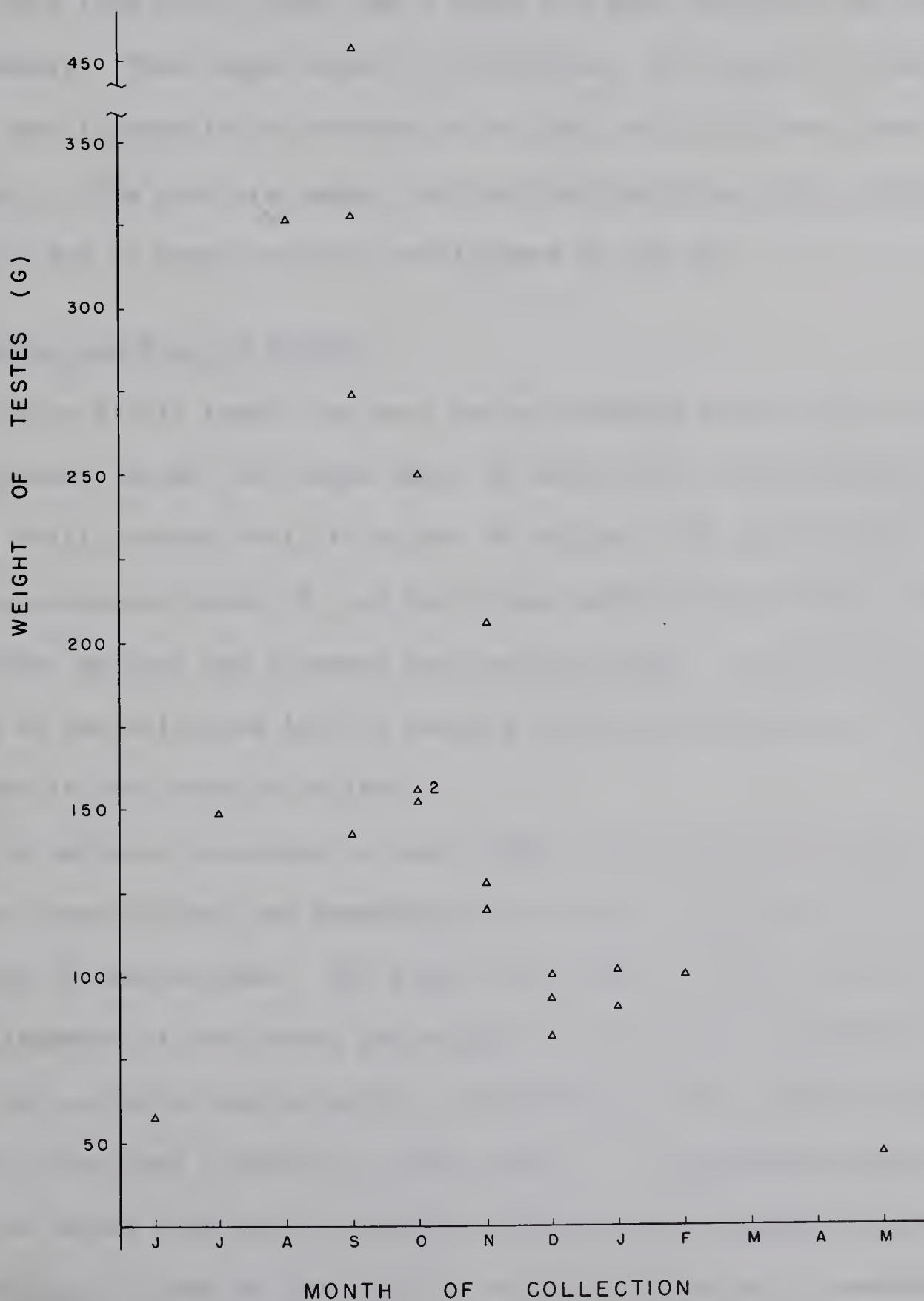


Fig. 12. Abundance of spermatozoa in smears of testis and epididymus, and weight of testes of individual wapiti 3 years old and older, according to month of collection, Banff and Kootenay National Parks. Each number beside plotted symbol represents number of specimens if in excess of one.

ABUNDANCE OF SPERMATOOZOA
(ARBITRARY RATING)

AGE \geq 3 YEARS

○ EPIDIDYMISS
● TESTIS



mount a cow and copulate, Struhsaker (1967) found that the participation of the young classes of males in rutting activities was slight. The five instances of completed copulatory mounting which Struhsaker observed were all performed by bulls older than 3-year-olds. He observed 348 heterosexual approaches by males older than 3-year-olds, only 6 such approaches by 2-year-olds, and 14 by yearlings.

Only five bulls older than 2 years old were collected in the month of September. Their ages, dates of collection, the weights of their testes, and information on whether or not they were with cows, are given in Table 4. The data are meager but they indicate that bulls between the ages of 7 and 12 years actively participate in the rut.

Replacement and Size of Antlers

Murie (1951) found that most antler shedding took place in March. In the present study, two males about 22 months old, collected March 28 and 30, still carried their first set of antlers, but another male of the same age collected March 28, and two 2-year-olds collected June 2 had shed their first antlers and produced new vascular knobs. A bull approaching 3 years of age collected April 2 carried its old antlers but an adult taken May 24 had vascular antlers.

In antlers, according to Goss (1963), the hardening of the bone, vascular constriction, and shedding of the velvet are controlled by secretion of testosterone. The close coincidence of those events with the enlargement of the testes was evident in this study (Appendix 6).

The period of antler growth and shedding of the velvet in yearlings was later than that observed in older wapiti. A 10-year-old animal collected August 19th was the earliest observed with polished antlers. Two other adults seen on the same day carried antlers still completely

Table 4. Harem associations and weights of testes, in relation to age of bulls collected in September, Banff National Park

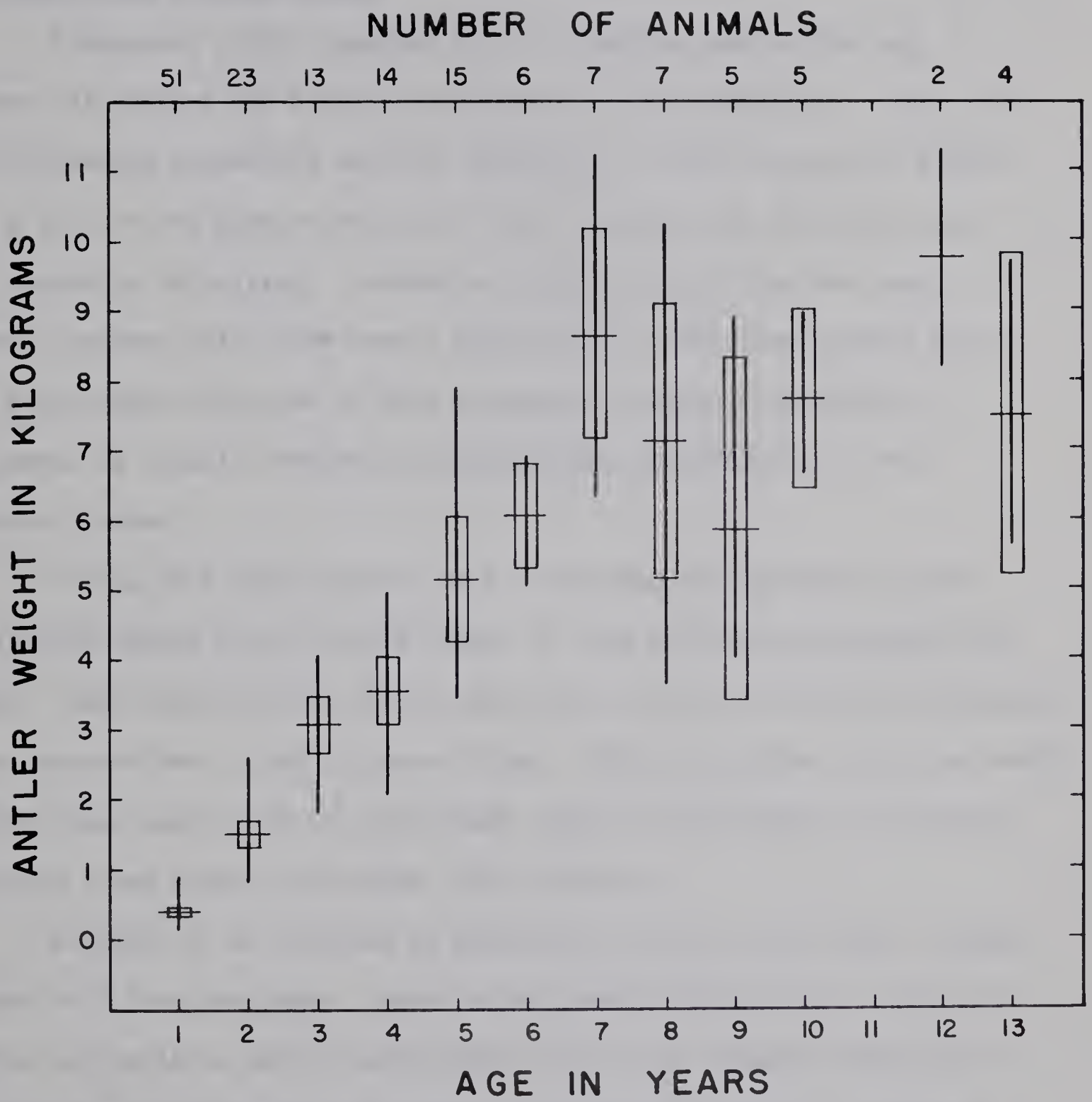
Date	Age (yr)	Weight of testes (g)	Association
Sept 8, '65	7	455	Harem
Sept 11, '61	5	274	Solitary
Sept 12, '61	9	143	Solitary
Sept 15, '61	8	328	Harem
Sept 27, '65	12	357	Harem

covered with velvet. All adult and 2-year-old bulls collected after September 8 had polished antlers. However two yearlings taken September 14 and one taken October 15 had antlers that were still vascular and in velvet, and the earliest that a yearling with hardened antlers was collected was October 14. Although the antlers of all yearlings collected after October 15 were hardened, some retained all or part of their velvet covering until they were shed in the spring. Murie (1951) observed the same condition in some yearlings.

Data on the weights of antlers of wapiti taken in the slaughters in Banff in 1960-61, 1961-62, and 1962-63 are presented in Fig. 13. Mean antler weight increased with each successive year of age from the yearling class to 7 years old. Although the mean antler weight of 6-year-olds was significantly smaller than that of 7-year-olds, it was not significantly smaller than that of all specimens 7 years and older. The mean antler weight of 5-year-olds was, however, significantly smaller than that of all older animals. The graph suggested a decline in antler weight following 7 years. However, statistical comparison of the group 8 to 13 years old with the 7-year-old class did not show a significant difference.

Statistical comparisons show that the youngest age class which was not significantly smaller in antler weight than all older animals was the 6-year-old class, while the youngest age class that belonged with the adult group homogeneous in body weight, was the 5-year-old class. However, the configurations of the graphs in Figs. 9 and 13 suggest that peaks of both body weight and antler weight may not be reached until 7 years of age. Huxley (1931) found that the weights of successive sets of antlers, as well as the body weights of red deer stags in an English park, increased in relation to age until both reached peaks at about 10 years and declined

Fig. 13. Weight of antlers of wapiti of each age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.



thereafter. The size of antlers produced annually, body weight, and reproductive activity might all be expected to decline in old age as part of the process of senescence.

Mortality from Rutting Combat

Struhsaker (1967) observed that in sparring during the rut, almost all contact was between the antlers of the combatants. Only once in 49 sparring encounters which he observed in detail during one season, was a blow to the body noted, and in that instance the recipient did not appear to be injured. Struhsaker noted that sparring was more intense between bulls that were 3 years old or older than younger males, and particularly when one of them possessed a harem. Apparently dominance is usually resolved without injury, particularly in the younger classes.

During this study reports of six instances of mortality caused by rutting combat were received (Table 5), one of which was outside the parks. Each wapiti killed was an adult bull. The two from which dentaries were obtained were 7 and 12 years of age. While the number found was small, neither were many found of which death could be attributed to any other specific cause except collisions with vehicles.

Evidence of an increase in mortality of males after about 7 years of age will be given later. Data on the relationship of age to size of testes and antlers, and to association with harems suggest that bulls 7 years old and older may be the most reproductively active. It will be shown later that males older than 7 years enter the winter with lower fat reserves than other wapiti and are probably therefore more prone to winter mortality. The relationship of fat depletion to rutting activity

Table 5. Bull wapiti killed in rutting combat

Date	Locality	Remarks	Observer
Sept 15, '58	Banff	Adult, neck broken	G. A. Balding*
Sept '59	Lac La Biche Alta	Adult, abdomen torn	D. Kerik†
Sept 3, '60	Jasper	Large adult, lungs punctured	W. Measor*
Autumn, '65	Waterton Lakes	Adult, body punctured	E. B. Cunningham*
Sept 7, '66	Jasper	12-yr-old, body punctured, testes torn out	F. Burstrom*
Sept 19, '66‡	Jasper	7-yr-old, left eye knocked out, left side chest punctured	N. Young*

* National Parks Service

† Alberta Fish and Wildlife Division

‡ Still living when found, shot

will be discussed. Rutting combat, although it almost certainly removes fewer bulls than winter mortality, is evidently selective for the age of greatest sexual activity and should not be discounted as an influence on population dynamics.

REPRODUCTIVE CHARACTERISTICS OF THE FEMALE

In wapiti taken in slaughters beginning December, 1957 in Jasper, December, 1958 in Banff, December, 1960 in Elk Island, and January, 1963 in Waterton Lakes, uteri were inspected, and if enlarged were opened to determine the number and sex of fetuses. During some slaughters, the mammae were incised and inspected for the presence of milk.

All fetuses from cows slaughtered in Banff in November and December, 1966 and in Jasper in December, 1966 and January, 1967 were preserved in 10% formalin. Foetal length was measured as described by Morrison, Trainer, and Wright (1959). As was suggested by Morrison *et al.*, their graph relating foetal length to age was enlarged. The age of each foetus was estimated from the graph, and the conception date extrapolated by back-dating from the date of collection.

Age-specific Pregnancy Rate

The percentages of cows pregnant in samples taken from different parks and in different years from December 1957 to January 1967 are shown in Table 6. Females older than yearlings are combined. No calves examined were pregnant. The pregnancy rate in samples of yearlings varied greatly (0-78%) even in samples taken in the same park in different years. Among samples of cows 2 years old and older the pregnancy rate was high and fairly consistent. Evidently the development of breeding condition by yearling females is more subject to the effects of environmental conditions than is the case among adult females. The same relationship has been reported among white-tailed deer fawns (Cheatum and Severinghaus, 1950; Ransom, 1967) and yearlings (Ransom, 1967) and mule deer yearlings (Julander, Robinette, and Jones, 1961).

Table 6. Pregnancy rates according to park and year in cow
wapiti slaughtered in Elk Island, Jasper, Banff, and
Waterton Lakes National Parks, 1957 to 1967

Park	Year	Age 1 year		Age ≥ 2 years	
		Pregnant (%)	Number examined	Pregnant (%)	Number examined
Elk Island	1960	0	18	97	31
	1963	29	7	93	28
Jasper	1957-58	71	7	100	27
	1963-64	0	17	95	106
	1966-67	78	9	92	107
Banff	1958-59	29	7	94	36
	1959-60	23	13	91	140
	1960-61	16	19	97	101
	1961-62	8	12	92	100
	1962-63	13	15	96	92
	1963-64	50	4	92	41
	1964-65	29	7	82	88
	1965-66	0	1	88	24
	1966-67	50	4	81	32
Waterton Lakes	1963	50	12	100	59
Total		24	152	93	1012

Buechner and Swanson (1955) reported a pregnancy rate of 54% in a sample of 35 yearling wapiti in the Blue Mountains of Oregon. They suggested that the high rate of natality could be attributed to a reduction in the density of the population by heavy hunting. Hancock (1955) reported that six yearlings of seven examined were pregnant in hunted populations in Utah. Prior to the above studies, observations of pregnant yearlings had been so uncommon as to be considered noteworthy. Mills (1936) reported one yearling pregnant among five examined in Yellowstone Park. Murie (1951:123) found no pregnancies in, "a large number of so-called yearling cows", examined, presumably in Yellowstone Park and Jackson Hole. Kittams (1953) found one yearling cow pregnant among 39 examined in Yellowstone. Coffin and Remington (1953) reported one yearling pregnant among seven examined in Rocky Mountain National Park, Colorado, and Saunders (1955) reported a single observation of a pregnant yearling in Montana. Perhaps the scarcity of such observations prior to 1955 is not surprising inasmuch as the ranges where extensive data had been collected were depleted and heavily stocked (for example Jackson Hole, see Anderson, 1958 and see Kittams, 1953).

Pregnancy rates in samples of cows older than yearlings, reported in the literature, are generally high. Murie (1951) reported that of 334 cows, "of breeding age", from Jackson Hole and 156 from Yellowstone, 89.2% and 90.4% respectively, were pregnant. Kittams (1953) reported that pregnancy rates in samples of cows 2-1/2 years old and older slaughtered in five different years in Yellowstone varied from 74% to 94% with a mean of 85%, in a total of 1,053 specimens.

Green (1950) examined wapiti taken in slaughters in Banff between 1944 and 1948 and reported no pregnancies among 47 yearlings, and 78%

pregnant among 632 females 2-1/2 years old and older. However, by Green's method of age determination (Green, 1946; Banfield, 1949), all specimens with more than one pair of permanent incisors would have been included in the older class. Quimby and Gaab (1957) found that the second pair of incisors had been replaced in a substantial proportion of yearlings collected in winter. There may, therefore, have been yearlings among the pregnant animals reported by Green (1950), and as there were almost certainly some non-pregnant yearlings among the animals which he assigned to the group 2-1/2 years old and older, the pregnancy rate in the group actually 2-1/2 years old and older was probably higher than reported.

When the pregnancy rate among yearling cows is compared with that among older cows in the total sample examined in this study (Table 6), using the χ^2 test (Simpson, Roe, and Lewontin, 1960:187), a significant difference ($P < 0.005$) is indicated.

In Table 7, data collected in slaughters in all parks from November 1961 to January 1967 are consolidated to show the percentages of cows pregnant at different ages. It is evident that from 2 to 13 years old the pregnancy rate was consistently high, followed by a slight decline at about 14 years. Among 632 cows examined in the group 2 to 13 years old, 592, or 94% were pregnant. In comparison, among 44 cows examined in the group 14 to 19 years old, 30, or 68% were pregnant. The latter rate is significantly lower ($P < 0.005$).

Multiple Pregnancies

Only two multiple pregnancies were found in 1,186 gravid uteri examined during this study, both were from Jasper. Both were sets of female twins, one carried by a 2-year-old shot in December, 1963, and the other, by an 8-year-old shot in December, 1966. Kittams (1953) after

Table 7. Pregnancy rates according to age in cow wapiti
slaughtered in Elk Island, Jasper, Banff, and
Waterton Lakes National Parks, 1961 to 1967

Age (yr)	Pregnant (%)	Number examined
1	27	88
2	93	115
3	97	98
4	92	76
5	92	64
6	90	71
7	94	49
8	94	36
9	94	50
10	97	29
11	100	17
12	100	12
13	87	15
14	77	13
15	73	11
16	75	8
17	60	5
18	20	5
19	100	2

consolidating published and unpublished data reported, "All available quantitative records of the Rocky Mountain elk total 1,690 pregnancies with 5 twinnings". Reports from Waterton Lakes quoted by Cowan (1950) placed the percentage of twins among wapiti calves in that area at between 20 and 25%. However, the uteri of 199 pregnant cows slaughtered in that park between 1949 and 1962 were opened by park personnel to identify the sexes of foetuses. As no twins were recorded in that sample, it seems likely that the information reported to Cowan was based, as Kittams (1953) suggested, on calf-at-heel observations, which can be misleading. It can be concluded that even under favorable environmental conditions, multiple pregnancies are very rare in wapiti.

Duration of Lactation

Data on the condition of the udder were collected from cows slaughtered in Banff, December, 1958 to December, 1967, and in Jasper, December, 1966 to January, 1967. The incidence of lactating condition among cows 3 years old and older shot in each of the 3 months, November through January, was tabulated separately (Table 8). This gives an indication of when lactation was usually terminated. In the total sample from Banff, cows shot in December included a similar proportion of lactating specimens as did those shot in November. However, the proportion of cows lactating among January specimens was significantly lower ($P < 0.005$) than among those taken in November and December. With the exception of the samples taken in November, 1966 in Jasper, and December, 1965 in Banff, both of which were very small, the samples from individual slaughters conformed to the pattern shown by the total sample.

Kittams (1953) showed consistent, statistically significant decreases in the percentage of lactating specimens among cow wapiti 3-1/2 years old

Table 8. Percentages of cows lactating, according to month, among wapiti 3 years old and older, Banff and Jasper National Parks

Park	Year	November		December		January	
		Lactating (%)	Number examined	Lactating (%)	Number examined	Lactating (%)	Number examined
Jasper	1966-67	25	4	65	43	40	35
Banff	1958-59	-	-	69	29	60	5
	1959-60	-	-	60	53	42	60
	1960-61	-	-	57	49	36	39
	1961-62	64	31	67	36	36	14
	1962-63	-	-	67	52	43	23
	1963-64	-	-	71	24	57	7
	1964-65	61	33	62	16	57	28
	1965-66	58	19	17	6	-	-
	1966-67	68	25	75	4	-	-
Banff Total		63	108	66	240	43	171

and older slaughtered in Yellowstone in successive weekly periods in 1949-50, from 46% in the week beginning December 19, to 31% in the week beginning January 11. The decreases indicate that weaning was in progress at that time. In 1951 he noted incidences of lactation of 16%, 18%, and 14% for the three successive one-week periods beginning January 3. Both higher calf survival and later weaning could have contributed to making the incidence of lactating cows higher among those from Banff and Jasper than in the Yellowstone samples. As Kittams described widespread deterioration of the Yellowstone winter range, the differences may have been related to nutritional levels. The data from Banff and Jasper demonstrate that few cows terminated lactation in November or December but that a substantial proportion did so in January.

Age-specific Incidence of Lactation

Milk in the udder is evidence that a cow was suckling a calf at least until shortly before the time of examination. As it has now been shown that few if any cows terminated lactation during November and December, the data on incidence of lactation in those months provide a measure of the proportion of cows that had calves living at that time of year.

As was anticipated in view of the absence of pregnant calves, none of the yearlings examined were lactating. Percentages of cows lactating at different ages older than yearlings are given in Table 9. The data used are from slaughters in Banff from November, 1961 to December, 1966, and in Jasper in November and December, 1966. Samples from other slaughters were not used because the animals were shot after January 1, or because the data were incomplete. Among the 2-year-olds, 11% were lactating. Percentages of cows lactating in individual age-classes from 3 to 14 years old do not indicate any change within that age range. Among the 268 cows 3 to 14 years

Table 9. Percentages of cows lactating according to age, in samples* slaughtered prior to weaning, Banff and Jasper National Parks

Age (yr)	Lactating (%)	Number examined
2	11	53
3	64	36
4	55	31
5	72	36
6	65	34
7	67	33
8	70	20
9	75	24
10	71	17
11	50	10
12	64	11
13	43	7
14	67	9
15	0	4
16	67	6
17	60	5
18	25	4
19	0	1

* Banff, November, 1961, 1964, 1965, and 1966, December, 1961 to 1966, and Jasper, November and December, 1966.

old 65% were lactating. As was anticipated in view of the decline in pregnancy rate noted at 14 years of age, the data indicate a decline in the frequency of lactating cows at 15 years. Of the 20 cows 15 to 19 years old, only 8, or 40% were lactating which is significantly lower than among younger cows.

By dividing the percentage of cows lactating by the pregnancy rate, the rate of survival of calves from about 3 months post-conception to about 6 months post-parturition can be estimated. Survival was estimated thus for calves in Banff, using data from the slaughters from November, 1961 to December, 1966, with January data on lactation excluded (Table 10). That determination does not take into account any losses of fetuses or calves that are associated with mortality of the dams. The computed rate of survival of calves carried by cows of all ages was 69%. In neither the 2-year-old group (yearlings at conception) nor the group 15 years old and older (≥ 14 years at conception) was the number of cows lactating significantly lower than the number expected on the basis of the observed pregnancy rate and a calf survival rate equal to that of dams 3 to 14 years old (2 to 13 years at conception).

It was shown previously that yearling cows, and those 14 years old and older exhibited lower pregnancy rates than cows 2 to 13 years old. However the above analysis suggests that both yearlings and cows 14 years old and older, which became pregnant and survived the following year, were as successful mothers as were cows in the intermediate age group.

Distribution of Dates of Breeding and Calving

Morrison (1960) reported an average estrous interval of 21 days for a group of captive wapiti. Two periods of estrus in one season were

Table 10. Calf survival from approximately 3 months post-conception to 6 months post-parturition, as estimated from pregnancy rate and frequency of lactating specimens among cow wapiti* slaughtered, Banff National Park, November, 1961 to December, 1966

Age of dam at conception (yr)	Pregnancy rate (%)	Frequency of lactation (%)	Calf survival (%)
1	21 ₍₄₃₎	13 ₍₄₆₎	62
2-13	92 ₍₃₄₀₎	67 ₍₂₂₅₎	73
≥14	71 ₍₃₈₎	40 ₍₂₀₎	56
≥1	83 ₍₄₂₁₎	57 ₍₂₉₁₎	69

*January data on lactation excluded.

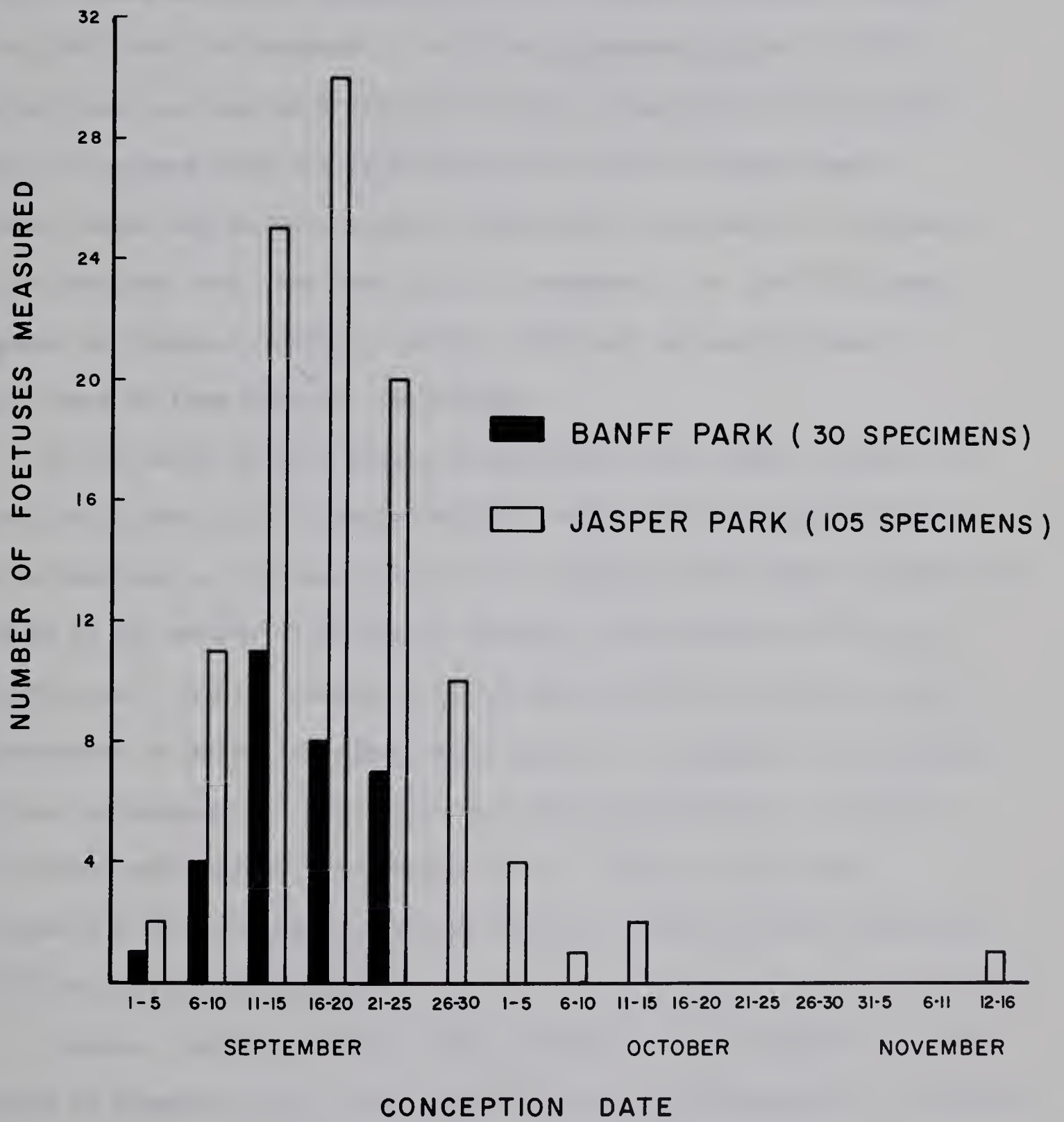
Values in parentheses are numbers of specimens examined.

the most that were specifically mentioned by Morrison (1960). However the cows used in that study were enclosed with a fertile bull after their first estrus and most of them conceived in their second.

The distribution of conception dates of wapiti in Banff and Jasper in 1966 as estimated from foetal lengths is presented in Fig. 14. The conception dates of all specimens from Banff except one were within the period September 6 - 25, which coincides closely with Struhsaker's (1967) findings in that area in 1965. He showed a peak of heterosexual activity between September 8 and September 21. The mean estimated conception dates in 1966 were September 11 in the case of the Banff sample, and September 19 in the case of the Jasper sample. Those are significantly different. The mean conception date for 6 yearlings from Jasper Park was September 28 as compared to September 18 for older cows, but the difference is not significant. The one November conception occurred in a 5-year-old cow.

Morrison *et al.* (1959) reported a gestation period of 247 days for one cow of which the breeding dates of the dam, and the birth date were known. According to Lantz (1910) as quoted by Murie (1951), the gestation period of wapiti is from 249 to 262 days. Using the midpoint, 256 days, and the mean estimated conception dates of September 11 in Banff and September 19 in Jasper the mean birth dates in 1967 would have been May 24 and June 1 respectively. Johnson (1951) reported that for 158 calves examined soon after birth in the West Gallatin River drainage of Montana, the peak period of birth was June 1, and the extremes were May 21 and June 12.

Fig. 14. Distribution of conception dates of wapiti, Banff and Jasper National Parks, 1966, as estimated from lengths of fetuses and dates of slaughter of dams.



Foetal Sex Ratio

Useable data on the number of fetuses of each sex carried by wapiti slaughtered in all parks during the present study are given in Table 11. Data on sex of fetuses from Elk Island in December, 1958, and in 1959 prior to December 3, and from slaughters prior to 1963 in Waterton Lakes are excluded because in those slaughters a substantial number of fetuses were not identified as to sex, and among small fetuses, males may be more readily identified than females. Similarly, data on fetuses from cows shot prior to December 3 in the Elk Island slaughter of November, 1959 to January, 1960 are excluded because a large number of them were not identified.

In the total of 1159 fetuses included in the sample, (Table 11) the sex ratio was 113:100 (males:females) which differs significantly from an even ratio. The sex ratio of 462 fetuses from wapiti slaughtered in Banff in the months of November, December, and January 1944-48 was 111:100 (Green, 1950). Bourlière (1964:296) pointed out that an early preponderance of males is common among species of ungulates and pinnipeds which are polygynous and which have a strong preponderance of females in the adult populations. Robinette *et al.* (1957) consolidated published and unpublished data on the sexes of 2,299 mule deer fetuses, and the sex ratio was 111:100.

Chapman, Casida, and Cote (1938) showed that in a sample of 2,044 fetuses of domestic cattle, the proportion of males decreased in relation to advancing gestation. Robinette *et al.* (1957) presented data on mule deer which suggested that when adverse circumstances affect the dams, male fetuses may be more prone to mortality than females. In view of those findings, it seems likely that in wapiti the ratio of males to

Table 11. Numbers of fetuses of each sex from wapiti slaughtered
in Jasper, Banff, Waterton Lakes, and Elk Island National
Parks

Park	Period of slaughter	Fetuses			
		Males (no.)	Females (no.)	Too small to identify (no.)	Ratio (♂:♀)
Jasper	Dec, '57	22	14	0	
	Dec, '63-Jan, '64	54	50	2	
	Nov, '66-Jan, '67	61	46	1	
	Total	137	110	3	124:100
Banff	Nov-Dec, '57	11	12	0	
	Dec, '58-Jan, '59	24	15	1	
	Dec, '59-Jan, '60	67	70	0	
	Dec, '60-Jan, '61	54	49	0	
	Nov, '61-Jan, '62	58	39	0	
	Dec, '62	38	52	1	
	Dec, '63-Jan, '64	20	20	0	
	Nov, '64-Jan, '65	44	32	5	
	Nov, '65-Dec, '65	16	12	3	
	Nov, '66-Dec, '66	21	11	1	
	Total	353	312	11	113:100
Waterton Lakes	Jan-Feb, '63	33	35	1	94:100
Elk Island	Dec, '59-Jan, '60	59	52	1	
	Dec, '60	16	14	4	
	Dec, '63	18	20	1	
	Total	93	86	6	108:100
All parks	Total	616	543	21	113:100

females would be equal to, or slightly higher than, 113:100 at conception and perhaps lower than that at birth. The following data on the sexes of wapiti captured within a few days after birth conform to the latter expectation. Johnson (1951) reported a sex ratio of 96:100 among 155 calves captured in the Gallatin River drainage in Montana and Yellowstone. Picton (1961) reported that a sample of 472 calves captured in the Sun River drainage of Montana contained 50.4% males which is equivalent to a sex ratio of 102:100.

Kittams (1953) presented data on the numbers of male and females among 1167 fetuses from wapiti shot in winter in Yellowstone and Jackson Hole. The sex ratio was 101:100 as compared to 113:100 in the present study. The pregnancy rate of cows 2 years of age and older in Kittams' sample was 86% as compared to 93% in the present study. That difference in pregnancy rate may have resulted largely from higher intra-uterine losses in the sample from Yellowstone and Jackson Hole, and male embryos may have predominated among those lost.

Miller (1932) mentioned a view held by a number of Scottish deer stalkers that female red deer which had not given birth the year previous, and those which lost their young and therefore ceased lactating, being in better physical condition, usually gave birth to male calves in the subsequent season. Of 405 red deer fetuses collected from Scottish estates, Miller was able to identify the sex of 271. Males were in the majority among fetuses from both lactating and non-lactating hinds, 51 of 79 in the former and 111 of 192 in the latter. Because the sex of so many fetuses could not be identified, Miller considered his data inconclusive.

The present data provide an opportunity to examine the possibility that lactation by the dam during pregnancy reduces the survival of male fetuses relative to female fetuses. Data presented previously indicate that many cows ceased lactating in January due to weaning. Therefore only

data on fetuses from wapiti shot before January 1 in slaughters held in Banff and Jasper were used in the comparison. The numbers of fetuses of each sex are presented in Table 12 according to the age of the dam and whether it was lactating. In each group the number of males exceeded that of females. There were no significant differences between the sex ratios of fetuses of cows of different ages, or between those of lactating and non-lactating cows. Thus, no influence of lactation on losses of male fetuses relative to female fetuses was indicated. However, cows slaughtered in Banff and Jasper were generally in good physical condition regardless of age or whether or not they were lactating, and the high pregnancy rates showed that if any intra-uterine losses occurred prior to the time of slaughter, the numbers of embryos lost were very small.

Table 12. Sex of fetuses according to age and udder condition of dam from wapiti shot in Banff and Jasper National Parks before January 1 in each slaughter November, 1957 to December, 1965

Age of dam (yr)	Presence (+) or absence (-) of milk	Foetuses		Sex ratio (♂♂:♀♀)
		Males (no.)	Females (no.)	
1	-	8	7	114:100
2	+	9	6	150:100
2	-	29	26	112:100
3	+	117	106	110:100
3	-	74	70	106:100
2	+	126	112	112:100
2	-	103	96	107:100

FAT RESERVES

On the basis of studies of large samples of red deer in New Zealand, Riney (1955) reported, "Examination of all the red deer used in this investigation showed that the first fat depot to respond to a favourable metabolic change was bone marrow, followed by the fat around the kidney, intestines, and stomach in that order, and finally, by the subcutaneous fat on the back. Mobilization of the fat depots observed was in reverse order to that of deposition."

Riney (1955) evaluated various techniques of determining the physical condition of red deer and concluded, "The kidney index (weight of kidney fat/weight of kidney) was the most satisfactory. This index showed how the fat-depot reserves in deer of both sexes and various ages changed during the seasons. It also showed that deer living in different environments had different quantities of fat reserves."

Seasonal Changes in Fat Reserves

For each animal in the research series, a kidney fat index was determined in a manner similar to that described by Riney (1955). Each kidney was removed from the carcass with its surrounding fat, and the fat was trimmed by two cuts passing against the anterior and posterior ends of the kidney at right angles to its longitudinal axis. The weight of the two kidneys and surrounding fat was measured to the nearest gram. The perinephric fat (*capsula adiposa*) along with the capsule of connective tissue (*tunica fibrosa*) beneath it were then peeled off the kidneys and the latter were weighed alone. The weight of the fat plus connective tissue was calculated by difference and expressed as a percentage of the weight of the stripped kidneys. The percentage was referred to as

the kidney fat index.

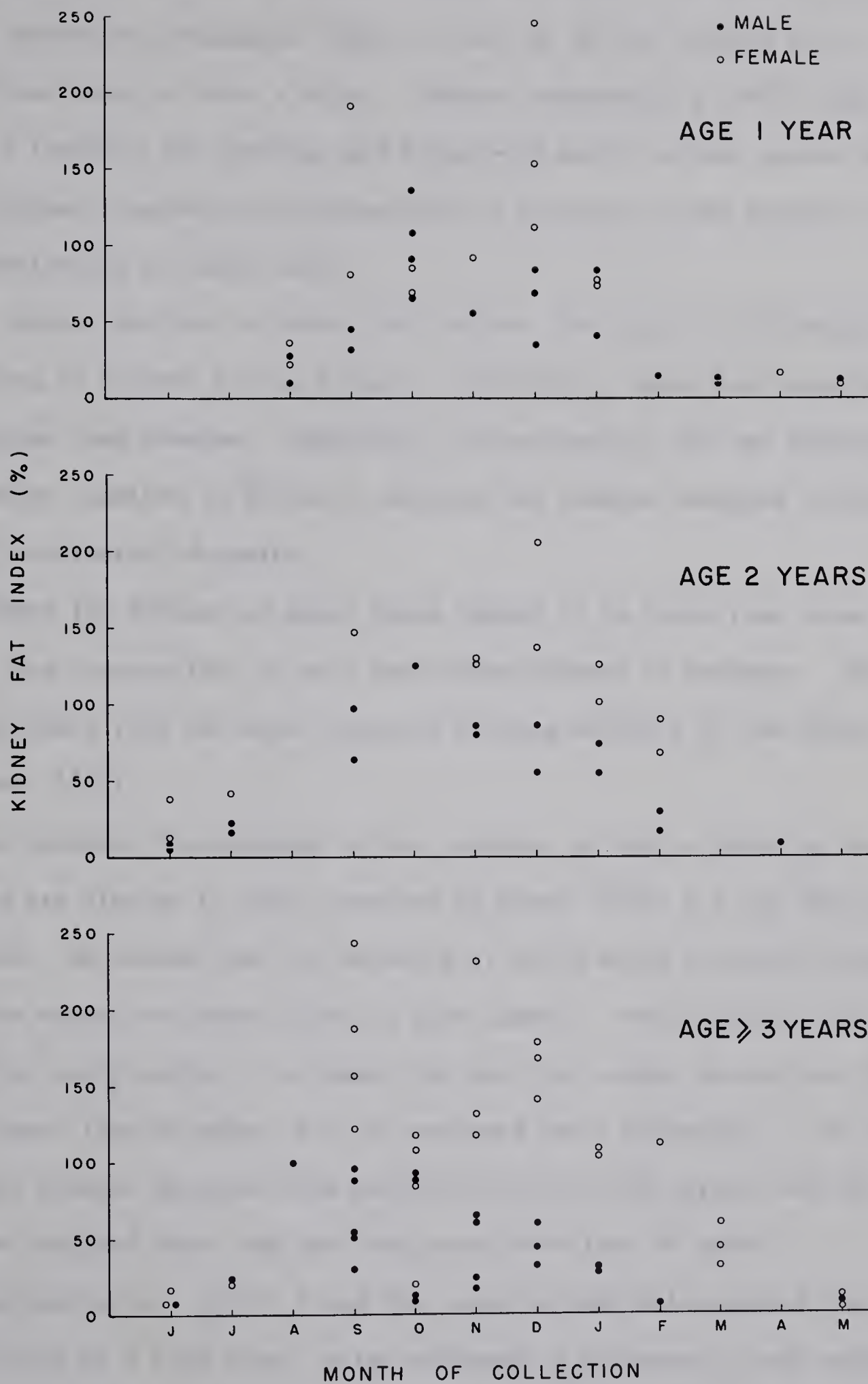
By including the weight of the capsule of connective tissue with the weight of perinephric fat, the indices were elevated slightly over what they would have been otherwise. An index of 5 or slightly higher indicated an absence of perinephric fat. The kidney fat indices are presented in Fig. 15.

Because the number of animals studied was small, data from those of various ages older than 2 years, and those collected in different years, were combined. That contributed to an individual variation in kidney fat indices. In spite of that high variation, the data demonstrate a seasonal cycle in fat reserves.

In all groups, the index dropped to a low in the spring from which it first showed substantial recovery in August and September. The indices in females were generally high from September through December. The one exception was specimen 103, a cow collected October 14, 1962, with a kidney fat index of 21. That specimen was 18 years old and had a large abdominal abscess. Indices in yearling and 2-year-old males were highest in October.

In adult males, high indices were observed in August, September, and October, but minimum values also occurred in the latter two months. A series of five bulls 7 to 12 years old, collected between August 19 and November 19, 1965, showed a consistent decline in kidney fat indices from the one collected August 19, to one collected October 19, with a partial recovery in the specimen taken November 19. In view of that pattern, it is suspected that variation associated with different ages and years obscured a decline in the fat reserves of adult males during the rut in September and early October. The data on yearling and 2-year-old males suggests a decline in November. Perhaps there is a delay in the

Fig. 15. Kidney fat indices of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks, and the Ya Ha Tinda Ranch.



decline in fat reserves in those two classes, as compared to adult males, that is related to a delay in their rutting activity. The data on testis size and spermatozoa abundance (Figs. 11 and 12) do not provide clear evidence that there is such a delay. However Struhsaker's (1967) data indicate a tendency for yearling and 2-year-old males to join groups of cows in October apparently concurrent with a decrease in the sexual arousal and aggressiveness of older bulls.

A general decline in kidney fat indices from early or mid-winter until spring is evident in all groups. In November, males had consistently lower indices than females. Similarly, the perinephric fat was exhausted in some males examined in February, whereas the females examined in March still had substantial deposits.

Kidney fat indices of adult bulls tended to be lower than those of yearlings and 2-year-olds, in each month from October to February. That probably results from the more intensive rutting activity of the adults (Struhsaker, 1967).

The seasonal fluctuations in fat reserves in wapiti shown by the above data are similar to those reported by Riney (1955) for red deer in New Zealand. He showed that fat deposits of adult males increased rapidly through the summer to reach a peak in late summer. They declined from autumn until early spring. In female red deer the summer deposition of fat was slower than in males, but it continued until mid-winter. The fat reserves of females declined from mid-winter until late spring, but the spring low occurred later and was less acute than that of males.

Magruder *et al.* (1957) found that captive male white-tailed deer fed *ad libitum* on a high level ration underwent a decrease in body weight during the middle and late rut in November and December. From December to

January there was little change, but a second decline occurred during February and March. The animals also showed a pronounced voluntary reduction in food consumption in autumn and winter. Their data suggest a time lag of about one month in the response of body weight to either an increase or a decrease in food consumption.

Wood *et al.* (1962) reported that captive male deer of various races of *Odocoileus hemionus* raised to 4 years old on *ad libitum* feeding exhibited a seasonal cycle in growth as measured by body weight. Body weight increased during late spring and summer, then declined from an early autumn peak to a spring low. The seasonal pattern of growth of female deer was similar to that of males. However, the magnitude of the fluctuations was less marked, and in the first 2 years of life the does did not lose weight in winter, but rather gained at a slower rate than in summer. Wood *et al.* found by dissection that an "appreciable part" of the spring and summer weight gain, and most of the winter weight loss consisted of adipose tissue. They reported individual differences in the exact date at which seasonal changes in the growth curve began. Differences similar to the above may have contributed to the variation in kidney fat indices observed among wapiti of one sex and age group collected in one month in the present study.

The observation here that kidney fat indices of adult male wapiti, when compared to those of other sex-age classes, tended to decline to lower levels during the rut, is entirely consistent with Struhsaker's (1967) behavioral observations. He showed that during the rut, bulls older than 3-1/2 years spent much less time feeding than any other sex-age class. Those that had harems, when compared to other sex-age classes, spent less than one-half as much time feeding, less time lying down, and

more time standing, walking, herding cows, thrashing woody vegetation with their antlers, digging with their antlers, and whistling, all of which activities with the possible exception of whistling, require considerable energy output.

Fat Metabolism of Bulls During the Rut

When examining wapiti collected in 1961 and 1962, it was noted that the livers of adult bulls collected during September and October were distinctly light in color and granular in appearance. Livers of males collected at other times of the year, and those of females collected at all times of the year were consistently dark red. Livers of yearling males collected in September and October were only slightly lighter in color than normal.

The possible physiological significance of changes in the liver during the rut was recognized later. Therefore, between August and November, 1965, five male and three female wapiti were collected in Banff. Large bulls with large antlers were selected so as to reduce variation associated with age. In addition, one adult male and one adult female collected in Riding Mountain National Park, Manitoba, in February, 1966 were included in this phase of the study.

Fresh liver samples were taken from each animal, sealed in polyethylene bags, and frozen on dry ice. They were analyzed for moisture, ether extractable lipids, crude protein, and iron. Also, cubes of liver, 5 mm on a side, were preserved in a 10% formalin. Frozen sections 30 microns thick were stained with Sudan IV, and after mounting, examined microscopically for fat droplets at 40X and 100X. Sections which showed more than traces of fat droplets were sampled by a line intercept method

at 40X using 20 randomly located transects, each 3.3 mm long and divided by means of an ocular disc micrometer into 100 lineal sampling units.

An additional measurement taken from the eight wapiti collected in Banff was the thickness of the subcutaneous fat measured at a point approximately 20 cm anterior to the base of the tail and 5 cm to the right of the mid-dorsal line.

The results of the studies of the liver samples are presented with corresponding data on kidney fat indices and rump fat thicknesses in Table 13. The rump fat measurements and kidney fat indices of the four bulls taken from August 19 - October 19 showed a marked decline in both fat depots with each successive specimen. The kidney fat index of the specimen taken November 19 showed considerable recovery of depot fat, whereas in the specimen taken February 10 it was lower, following the winter trend shown in Fig. 15. The relationship of the rump fat measurements to the kidney fat indices conformed to Riney's (1955) conclusion that the subcutaneous fat depots on the back followed the visceral depots in receiving fat under conditions of favorable metabolic change, and preceded them in being depleted under conditions of fat mobilization.

The fresh livers of the males collected September 8, September 27, and October 19, were distinctly light in color and granular in appearance, similar to those from males taken during the rut in 1961 and 1962. On close inspection of the surface of the liver or dissected interfaces, the granular effect was seen to be caused by dark areas on a light background. When slices of frozen liver from each of those three specimens were examined under a dissecting microscope after thawing, it was seen that the dark colored areas were the central areas of the hepatic lobules. The lobules refer here to the polygonal prisms in the center of each of

Table 13. Carcass fatness indices, and results of chemical analyses and histological examinations of livers of individual wapiti taken autumn and winter, 1965-66

Date	Spec no.	Age (yr)	Rump fat thickness (mm)	Kidney fat index (%)	Moisture (%)	Liver			Fat droplet abundance (%)*
						Protein	Percentage of dry matter	Fat	
<u>Males</u>									
Aug 19	106	10	70	100	69.5	70.7	0.08	8.2	Tr
Sept 8	107	7	25	94	69.0	57.9	.13	24.8	18
Sept 27	108	12	0	30	62.0	38.6	.05	49.8	38
Oct 19	110	12	0	7	63.3	56.0	.24	31.5	26
Nov 19	113	7	3	64	68.8	71.6	.16	14.3	4
Feb 10	RML	4	-	37	66.5	71.2	.10	11.6	Tr
<u>Females</u>									
Sept 29	109	4	38	244	69.7	71.6	.16	7.8	Tr
Oct 21	111	<1	10	146	66.7	65.6	.21	20.6	0
Nov 18	112	8	13	232	67.5	71.0	.11	13.2	0
Feb 9	RM2	4	-	131	75.5	71.5	.12	13.2	0

* Percentage of area of histological section showing stained fat.

which is an originating tributary of the hepatic vein referred to as a central vein (Bloom and Fawcett, 1962). The light colored areas were distributed around the outside of the lobules. When the tissue was covered with a film of water and the surface probed with a dissecting needle, droplets of clear fluid immiscible with water were released to the surface from the light colored areas.

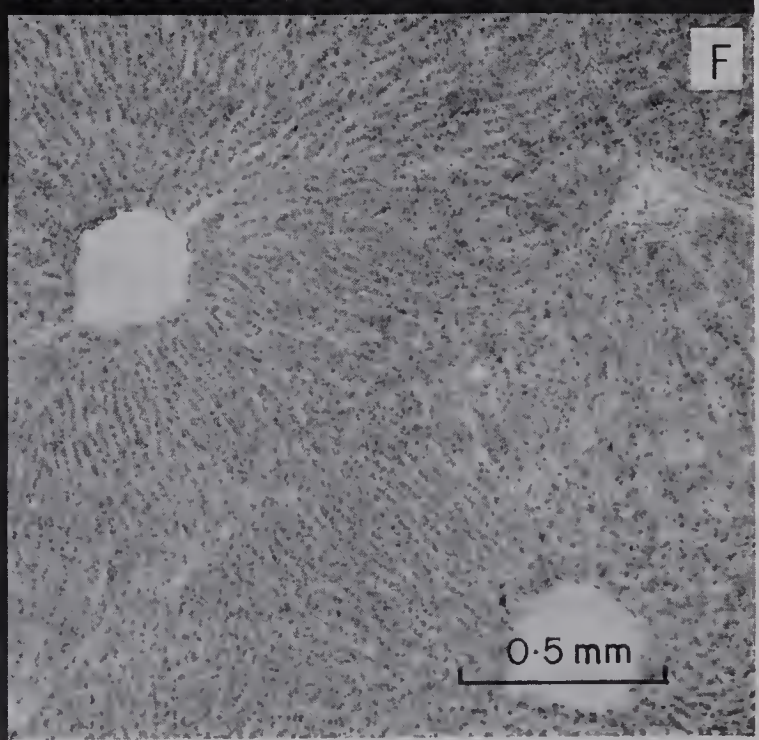
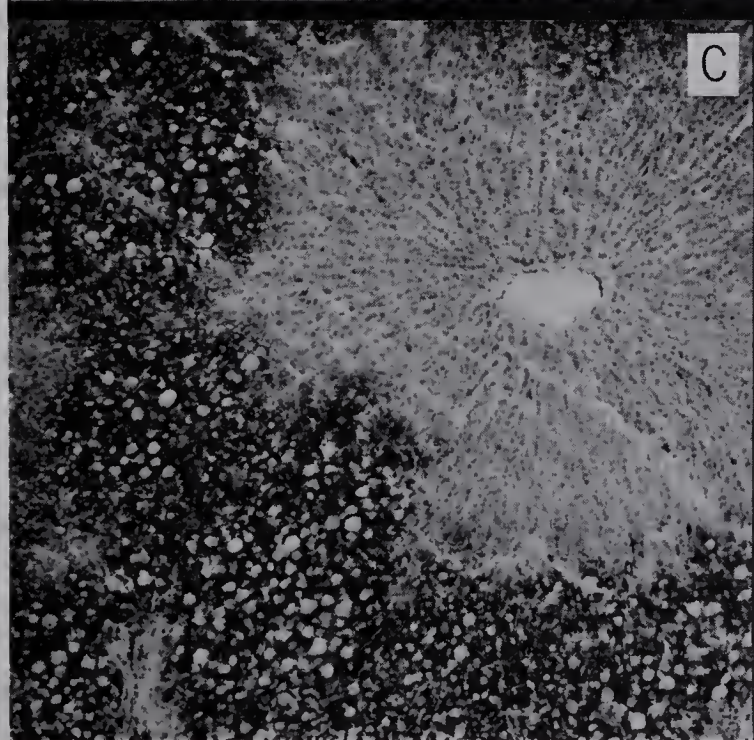
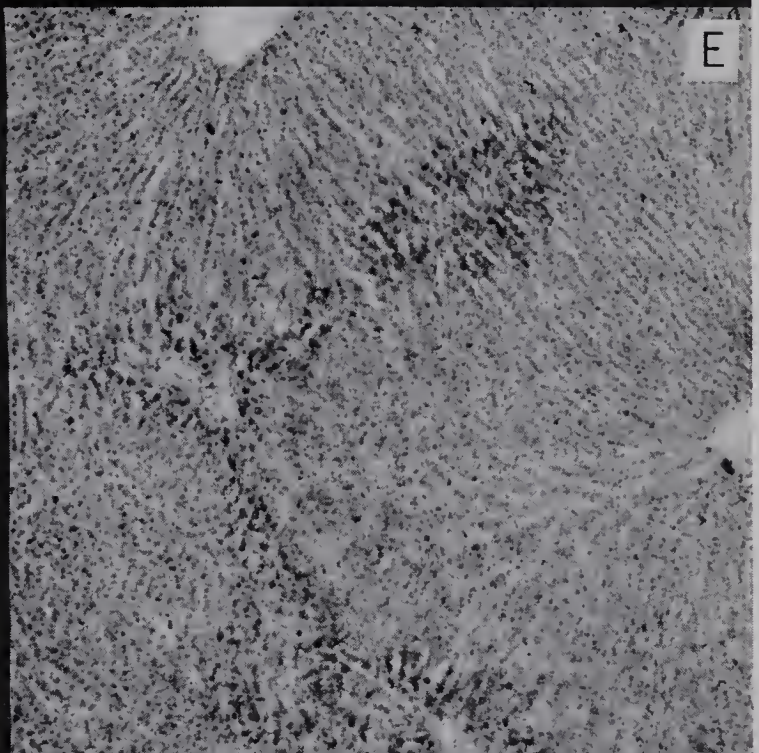
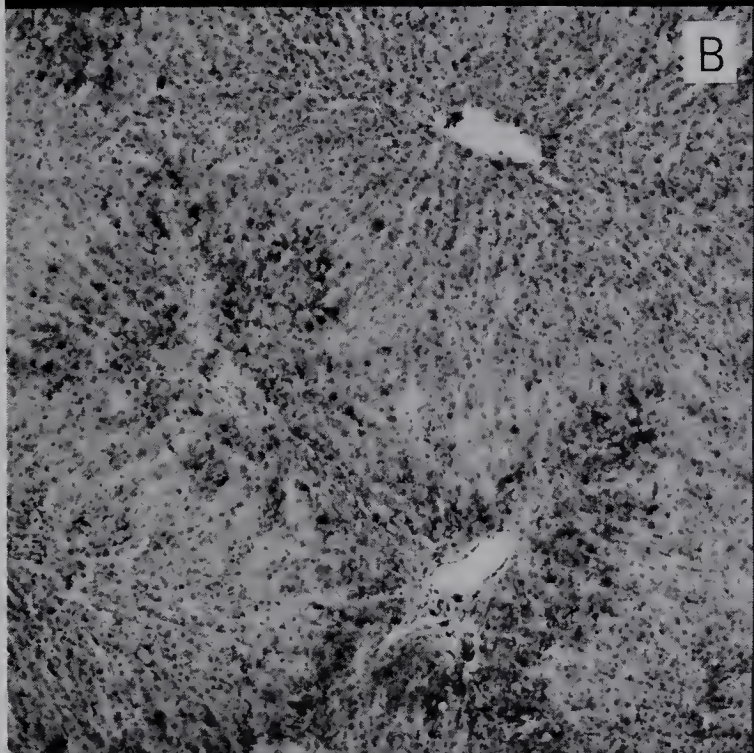
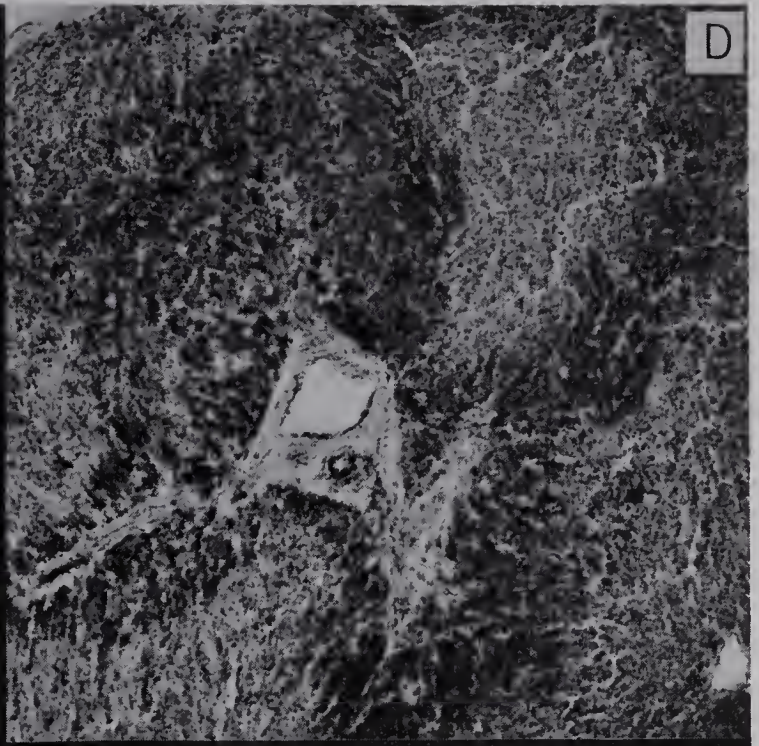
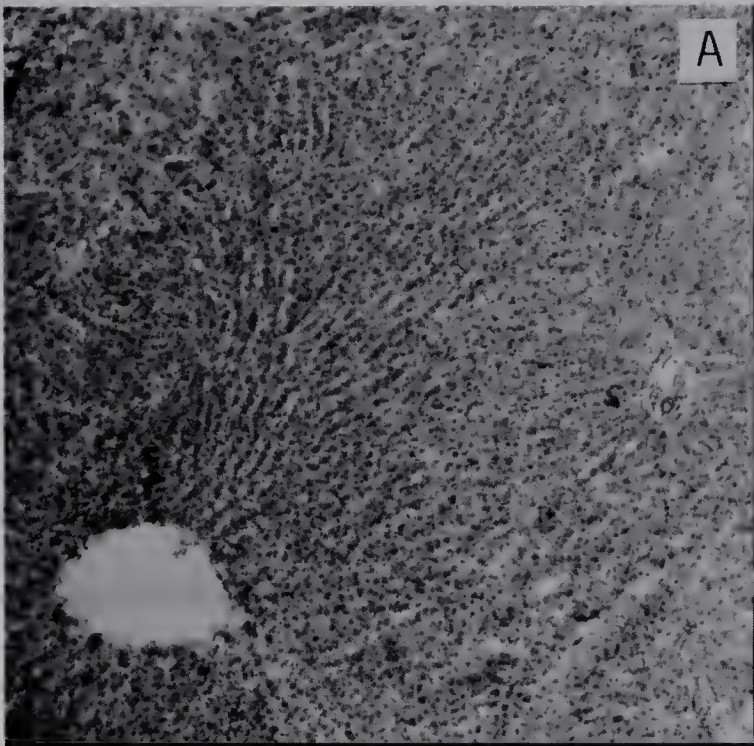
The fat content of the liver of males, as shown by ether extraction increased markedly with each successive specimen from August 19, to reach a peak in the specimen taken September 27, which is late in the rut. Following that, the fat content decreased with each successive specimen to reach a level in the November 19 specimen, that approximated that of the females. The liver samples from females did not exhibit a pronounced build-up in fat content during the rut. Specimen 111, a calf, had a liver fat content higher than that of other females. That may be a juvenile characteristic.

The percentage of protein in the liver tended to follow an inverse relationship to that of fat, but variations in the iron content did not appear to follow a consistent pattern.

Differences in the fat content of the liver as demonstrated by ether extraction were accompanied at high fat levels by corresponding trends in the abundance of stained fat droplets visible in histological sections (Table 13, and Fig. 16). In all cases the fat was distributed around the portal canals. In most samples of liver which had only a relatively low fat content, the histological preparations either failed to show stained lipid droplets or else showed only traces of them. In this regard Maximow and Bloom (1957:411) noted that there is a masking of much of the fat in liver cells which is an obstacle to using staining methods for estimating the amount of fat present. Similarly Wachstein

Fig. 16. Photomicrographs of sections of liver of wapiti from Banff National Park, 1965, stained with Sudan IV, showing sequence of physiological fatty infiltration in bulls during the rut. All photomicrographs have same scale as F.

- A. #106, ♂, 10 years old, August 19
- B. #107, ♂, 7 years old, September 8
- C. #108, ♂, 12 years old, September 27
- D. #110, ♂, 12 years old, October 19
- E. #113, ♂, 7 years old, November 19
- F. #109, ♀, 4 years old, September 29



(1963) stated , ". . . histochemical methods reveal only a small fraction of the total lipids in liver cells."

Thornton (1949:126) used the term "physiological fatty infiltration", to apply to the condition of accumulation of fat in the liver within limits in which the process is reversible. He reserved the term "pathological fatty infiltration" for the condition reached when fat accumulation is accompanied by damage to the hepatic cells. The condition observed in specimens 107, 108 and 110, which were bulls collected during the rut, can clearly be termed physiological fatty infiltration.

Barrett, Best, and Ridout (1938) showed by deuterium marking that fat depots are the major if not the only source of excess fat which accumulates in the liver during fasting. Dible and Popjak (1941) found that in the absence of depot fat, no fat will accumulate in the liver of a fasting animal. Steinberg (1963) reviewed the subject of regulation of fatty acid mobilization. The information contained in the following two paragraphs, which was extracted from his discussion, is basic to interpreting the fluctuations in liver fat observed in wapiti in this study.

Depot fat consists of triglycerides which are in a dynamic state, constantly being converted to free fatty acids that are released into the blood stream, and at the same time, being replaced by the conversion of free fatty acids to triglycerides. A decline in the concentration of glucose in the blood below a certain threshold, such as can occur in fasting, retards the conversion of free fatty acids to triglycerides, thus causing an increase in the concentration of free fatty acids in the blood, and therefore an increase in the rate of delivery of free fatty acids to the liver. Stimulation of the nerves supplying the fat depots has also been shown to increase the rate of mobilization of depot fat. In addition, a

number of hormones, including those secreted by both the medulla and cortex of the adrenal are known to stimulate the release of fatty acids.

In the liver free fatty acids are converted to triglycerides that are either secreted into the plasma as lipoproteins or oxidized. An increase in the rate of delivery of free fatty acids to the liver results in an increase in the rate of secretion of lipoproteins. However, even though the liver is functioning normally, the delivery of excessive amounts of free fatty acids to it can exceed its capacity to dispose of them by oxidation or resecretion as lipoproteins, in which case an accumulation of triglycerides in the hepatic tissue results. The liver, when it accumulates a large amount of fat, such as occurs in starvation or diabetes, may secrete ketone bodies into the blood.

As an explanation for the mechanism of ketosis, Krebs (1965) suggested that under certain conditions that demand a high rate of gluconeogenesis, much of the oxaloacetate made available in the liver is used in that process. The resulting fall in the level of oxaloacetate reduces the rate of completion of the carboxylic acid cycle for which it is also required. That leads to the production of ketone bodies, a process regarded by Krebs as an alternative type of respiration that in mild form is a normal physiological adaptation to a fall in blood sugar. Whether or not ketone bodies were being produced in any of the wapiti studied is not known.

It was evident that the high level of fat in the liver in adult bulls disappeared shortly after the rut without leaving any apparent liver damage. In view of Steinberg's (1963) discussion it seems fairly certain that the factors leading to the development of fatty liver among the adult males are the fat condition attained by them prior to the rut,

and their partial fast and high level of activity during the rut, as documented by Struhsaker (1967). Also, it might be expected that the high frequency and intensity of agonistic and heterosexual interactions in which the bulls participate during the rut would be associated with increased nervous and hormonal activity that would tend to stimulate mobilization of depot fat.

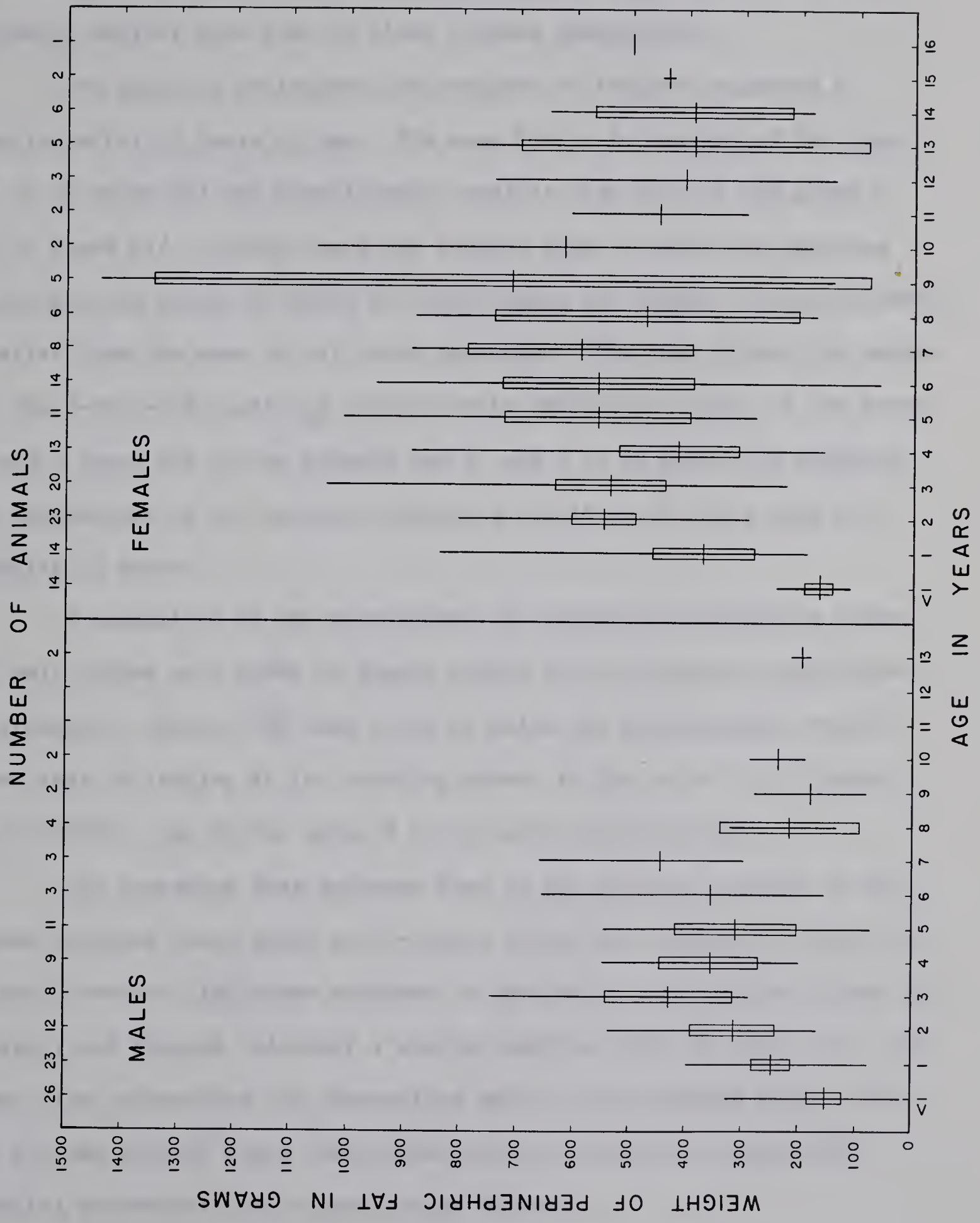
In the context of the welfare of the wapiti population, physiological fatty infiltration of the liver can be regarded as an annual event in the lives of the adult males, and a manifestation of the marked and rapid depletion of energy reserves which they undergo during the rut.

Differences in Fat Reserves Associated with Sex and Age

The kidneys and fat surrounding them were removed from the wapiti taken in slaughters in Banff in 1961-62 and 1962-63. The fat was trimmed in the same manner as described previously and the kidneys and fat were sealed in polyethylene bags and frozen. Later they were thawed and the perinephric fat with the capsule of connective tissue beneath it were removed and weighed. By weighing a few specimens before freezing and after thawing it was found that weight loss from the perinephric fat was negligible.

The data on perinephric fat weight of slaughtered animals are summarized in Fig. 17. These data represent the weights of the fat from the left and right kidneys together. In order to provide substantial samples of each specific age, data from November, 1961 through January, 1962, and December, 1962 through January, 1963 were consolidated. Inspection of the graph for males showed smaller mean values among animals 8 to 13 years old as compared to each age class from 1 to 7 years old. The mean perinephric fat weight of animals 8 to 13 years old was significantly smaller than the means of the groups 4 to 7, 3, to 7, or 2 to 7 years old.

Fig. 17. Weight of perinephric fat of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.





Within the group younger than 8 years old, the 2-year-olds were the youngest class in which the mean perinephric fat weight was not significantly smaller than that of older classes consolidated.

The graph of perinephric fat weights of females suggested a decline after 10 years of age. The mean kidney fat weight of the group 11 to 16 years old was significantly smaller than that of the group 2 to 10 years old. Within the group younger than 11 years the yearling class was the oldest in which the mean kidney fat weight was significantly smaller than the mean of all older specimens. The mean kidney fat weight of the 4-year-old class was significantly smaller than that of the group 2 and 3 years old or the groups 2 and 3, and 5 to 10 years old combined. No explanation of the apparent depressed condition of the 4 year old females is known.

A comparison of the mean kidney fat weight and confidence limits of male calves with those of female calves did not show any significant difference. However the mean value of males was significantly smaller than that of females in the yearling class, in the group 2 to 7 years old ($P < 0.01$), and in the group 8 to 13 years old ($P < 0.01$).

The foregoing data indicate that on the average, animals of both sexes attained their adult early-winter kidney fat weight at 2 years old. After 7 years of age males underwent a decline in early-winter kidney fat weight, and females underwent a similar decline after 10 years old. The data also corroborate the observation made in the research series, that in all age classes older than calves, males entered the winter with smaller perinephric fat deposits than females.

PARASITES

Data on the incidence of infections with certain parasites were obtained during the slaughters of wapiti conducted in Waterton Lakes in 1958-59 and in 1963, in Banff between 1958 and 1965, and in Jasper in 1963-64. The gross appearance of the liver of each specimen was noted, and, if there were discolored areas on the surface, the liver was sliced and inspected for the giant liver fluke (*Fascioloides magna*). (Some light infections may have been missed by that procedure.)

The lungs of all wapiti, except those slaughtered in Waterton Lakes in 1963, were inspected and palpated to detect hydatid cysts (the larval stage of the tapeworm *Echinococcus granulosus*). The bronchi of wapiti taken in Banff were opened with a boning knife or scissors to search for the thread lungworm (*Dictyocaulus viviparus*).

In the case of the research series, the following additional procedures were followed: The surfaces of the abdominal organs, the mesenteries, and peritoneum were cursorily inspected for nematodes or cysticerci of *Taenia* spp. The heart was sliced at 1-2 cm intervals to examine for cysticerci. In the course of removing the mandible, the masseter muscles were inspected for larval tapeworm cysts. The linings of the rumen and abomasum were examined cursorily for trematodes or nematodes. The duodenum, anterior 3 m of jejunum, and posterior 3 m of ileum were removed, each tied off separately, and the contents of each flushed out with water under pressure and screened for helminths. Similarly, the terminal 20 cm of the caecum, as well as a 25 cm section of the colon in the region where the faecal pellets are formed, were removed, tied off and the contents screened for nematodes. The tarsals, metatarsals, carpals, and metacarpals were skinned and examined for the deer legworm,

(*Wehrdickmansia cervipedis*). The nasal passages and retropharyngeal pouches were examined for larvae of the deer nose-fly (*Cephenemyia jellisoni*).

Skins of wapiti in the research series taken from September 1 through June and one taken in July, were sampled for ectoparasites as follows: A collar of skin, 25 cm wide, was removed from the neck immediately posterior to the ears. From all except those taken in December, two rectangular pieces of skin were also removed, one from each side of the body. They were 25 cm long by 12.5 cm deep, and located with the upper margin 12.5 cm below the dorsal mid-line, and so that they were bisected by the posterior rib. In a few specimens in which the skin from one side was rubbed or otherwise damaged in handling, samples were taken from only one side of the carcass. They were stored in separate bags, and processed by the technique of Hopkins (1940), in which the hair is digested by sodium hydroxide. Ectoparasites were screened out, identified and counted.

The giant liver fluke (*Fascioloides magna*) was found to be a common parasite of wapiti in Waterton Lakes, and Kootenay, and occurred with varying incidence in Banff.

The tapeworm (*Moniezia benedeni*), was noted in only one wapiti examined. That was a female calf shot February 16, 1962 on the Ya Ha Tinda Ranch and she carried two of those tapeworms in the anterior 3 m of the jejunum.

The fringed tapeworm (*Thysanosoma actinoides*), was found in the duodenum and jejunum of several specimens from Banff and Kootenay.

Hydatid cysts of the tapeworm (*Echinococcus granulosus*) occurred commonly in the lungs of wapiti in Banff and Jasper.

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The whipworm (*Trichuris ovis*), was noted in two wapiti. Two whipworms were screened from the ileum of a yearling male killed August 4, 1961 in the Cascade River Valley, and four, from the caecum of a yearling female collected on the same encounter.

The thread lung-worm (*Dictyocaulus viviparus*), was found to be fairly common in wapiti in Banff.

Only one peritoneal nematode, (*Setaria cervi*), was noted during the study. It was found near the ovary of a yearling female shot August 4, 1961 in the Cascade Valley.

Larvae of the deer nose fly (*Cephenemyia jellisoni*) were found in the pharynges of two specimens, a 23-month-old male taken March 30, 1962 in the Red Deer Valley which carried two larvae, and a female of the same age taken four days later in the Bow Valley, which carried five larvae.

Biting lice, (*Damalinia concavifrons*) were collected from skin samples of a few specimens from Banff and Kootenay, and the winter tick, (*Dermacentor albipictus*), was very common on skin samples from both of those parks. Complete data on ectoparasite infections are presented in Appendix 8.

No other parasites were found. Because of the limitations of the inspection of the surfaces of the adominal organs and the linings of the rumen and abomasum, helminth parasites in those areas could easily have been overlooked. More detailed information on infections by the parasites more commonly encountered will now be presented.

Giant Liver Fluke (*Fascioloides magna*)

Wapiti, moose, white-tailed deer, Columbian black-tailed deer and mule deer have all been reported as normal definitive hosts of this

parasite, while several species of snails have been found to act as intermediate hosts (Swales, 1935a; Cowan, 1951; Soulsby, 1965; 582-583).

Although the livers of 200 wapiti slaughtered in Jasper in 1963-64 were inspected, liver flukes have not yet been found in that park.

Among six wapiti, four males and two females, all older than calves, taken in Kootenay during late winter 1962, the livers of four contained liver flukes. Of the other two, the liver of one, a yearling male, had extensive scars, and that of the other, a 10-year-old female, had scars and encysted caseous remains of dead flukes. The only wapiti from Yoho National Park examined during the present study, a 2-year-old male shot in December, 1961 carried 5 flukes. This parasite was previously reported by Cowan (1951) in a moose and a mule deer in the Rocky Mountain Trench in British Columbia, where some wapiti from both Kootenay and Yoho migrate in winter.

Green (1946) reported that he examined the livers of 549 wapiti slaughtered in Banff in 1944-45 and 1945-46, for *Cysticercus tenuicollis*. The fact that he did not report liver flukes suggests that they were absent or uncommon in the park at that time.

No flukes were found in livers from 88 wapiti taken in the Bow Valley in the slaughter in December, 1958 and January, 1959. They were first recorded from Banff in wapiti examined by J. E. Stenton during the slaughter in December, 1959 and January, 1960. Incidences of liver flukes in the samples of wapiti older than calves slaughtered in the Bow Valley each year, from December, 1958 to January, 1965 are shown in Table 14. A marked increase in incidence during that period is evident. The samples slaughtered from December, 1959 to January, 1965 are consolidated in

Table 14. Incidence of giant liver fluke (*Fascioloides magna*) infections in wapiti older than calves examined in Bow Valley, Banff National Park, each slaughter 1958 to 1965

	1958 -59	1959 -60	1960 -61	1961 -62	1962 -63	1963 -64	1964 -65
Incidence (%)	0	2	4	5	4	21	50
No. examined	88	254	132	150	83	62	52

Table 15 to compare incidence of liver fluke infections according to sex and age of the host. Incidence among males and females was similar. No calves were infected and the incidence among yearlings was lower than among older age groups. Among age classes 2 years old and older the incidence of infection was fairly uniform.

In a sample of 339 wapiti from the Cascade and Red Deer drainages that were examined between December, 1960 and November, 1965, only two were infected with liver fluke. Both were males shot in 1962: a 2-year-old taken near the Cascade River in July, and a 6-year-old taken near the Red Deer River in Banff in December.

The previous absence of records of flukes from Banff, the scarcity of the parasite in those drainages of Banff farthest from the Kootenay drainage, the high incidence of infections in the sample of wapiti from Kootenay, and the uniform incidence of infections of liver fluke in different age classes of wapiti older than yearlings in the Bow Valley, all suggest that infected wapiti taken in Banff were infected immigrants from Kootenay. Occasionally wapiti have been observed crossing in either direction between the Kootenay and Bow drainages by way of Vermilion Pass. The rather heavy and consistent removals of wapiti from the Bow Valley, beginning in 1957, could be expected to have left space for occupancy by immigrants from the Kootenay drainage. In the latter area winter range is restricted, numbers of wapiti are fairly high, and the only wapiti harvested in Kootenay Park in recent years have been the six taken for the research series.

During the slaughter conducted in Waterton Lakes in 1958-59, fluke infections were found in 21% of a sample of 147 specimens. During the slaughter in 1959-60, fluke infections were noted to be common but the

Table 15. Incidence of giant liver fluke (*Fascioloides magna*) infections in wapiti of different age and sex examined in Bow Valley, Banff National Park, 1959 to 1965

Age (yr)	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
<1	0	78	0	60	0	138
1	7	68	5	58	6	126
2	14	37	12	80	13	117
3-5	10	89	12	162	11	251
6-9	8	47	16	105	14	152
≥10	9	11	15	53	14	64
≥1*	10	266	12	467	12	733

* Includes 14 males and 9 females the ages of which were assigned only as adult.

incidence was not recorded. The incidence of fluke infections among wapiti slaughtered there in January, 1963 is presented according to the sex and age of the hosts in Table 16.

The incidence among females was higher than that among males in the sample of each age group. The samples of males were small however, and when the incidences of infection in males and females were compared statistically within each age group, none of the differences were significant. However the incidence in the sample of all females older than yearlings was significantly higher than that of males of the same age group.

The tendency of males older than yearlings to range, much of the year, at higher elevations than females, (Cowan, 1950, and data to follow), probably reduces the opportunities for them to ingest liver fluke cercaria, as the latter are restricted to swampy areas and the margins of bodies of water suitable for the snails which act as intermediate hosts (Soulsby, 1965:583). This could have caused the observed sex difference in incidence of infections.

The incidence of liver fluke infections did not increase in relation to age in the sample of males. However, the number examined was very small. Females exhibited an increasing trend in incidence in relation to age, but the rate of increase declined with age. Of the female calves examined 33% had acquired infections leaving 67% not infected. Among female yearlings the incidence was 47% representing an increase of only 21% of the non-infected segment of calves. Furthermore there was an apparent decrease in incidence between 1 and 2 years of age, and only slight increases thereafter.

At least three circumstances could lead singly, or in combination, to the observed relationship of incidence of fluke infections to age.

Table 16. Incidence of giant liver fluke (*Fascioloides magna*) infections in wapiti examined in Waterton Lakes National Park, January, 1963

Age (yr)	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
<1	18	11	33	12	26	23
1	20	10	47	15	36	25
2	0	1	38	13	36	14
3-5	17	6	50	22	43	28
6-9	0	1	58	19	55	20
≥10	-	0	56	9	56	9
All ages	17	29	48	90	40	119

Those are: a counterbalancing of new infections by mortality selective for infected animals, a recent marked increase in exposure to infection, or an age-related resistance to infection.

Swales (1936) reported that the cervid host is protected from undue tissue damage by a capsule which it produces around the parasite. Swales (1935b) concluded that infections of giant liver fluke do not impair the health of the cervid hosts except in heavy infections, and that deaths of deer reportedly caused by it probably resulted from lowered resistance to other adverse circumstances under conditions of excessive infections. Similarly, Cowan (1951) reported that deaths in cervids caused by giant liver flukes were infrequent. However, Cheatum (1951), in comparing the incidence of liver fluke infections in white-tailed deer found dead in winter in New York to that in samples shot in the same areas, found that in adults the incidence was significantly higher in winter-killed specimens. As Cheatum did not include data to compare the ages of the two groups, there is a possibility that the winter-killed animals were older and the difference in incidence was age-related. In wapiti in Waterton Lakes, if the annual acquisition of new infections continued in adults at the same rate as occurred in the calves, selective mortality, in order to have prevented an increase in incidence of infection, would have had to be extremely heavy. As the age composition of the sample of females slaughtered in Waterton Lakes in 1962-63 (Appendix 19) indicates that mortality was not heavy between the yearling and 6-year-old classes, it seems doubtful that mortality was the main factor impeding an increase in fluke incidence in relation to age. However, with the information available, it is not possible to separate the effects of year-to-year variation in the opportunity for

infection, age-related resistance to infection, and mortality selective for infected animals, on the incidence of fluke infections in different age classes.

Fringed Tapeworm (*Thysanosoma actinoides*)

Cowan (1951) reported fringed tapeworms in a wapiti from Jasper, in two mountain goats (*Oreamnos americanus*) from Banff, and a bighorn sheep from Kootenay. This tapeworm has also been reported from wapiti, moose, mule deer, and Columbian black-tailed deer in other areas in western North America (Cowan, 1951; Honess and Winter, 1956; Barrett and Worley, 1965). Barklice or booklice of the order Psocoptera act as intermediate hosts (Allen, 1959).

The incidence of infections with fringed tapeworm found in wapiti in the research series taken at different times of the year are presented according to age and sex of the host in Table 17. Tapeworms were found in some specimens in every month in which autopsies were made except March and April. No specimens were examined in January. Within the limitations of the sample size there is little indication of seasonal differences in the incidence of this parasite.

There were no significant differences in the incidence of infections with fringed tapeworm between male and female wapiti, nor was there any significant difference in incidence between yearlings and 2-year-olds when data from animals of both sexes were combined. However, the animals 3 years old and older, of both sexes, had a significantly lower ($P < 0.005$) incidence than the yearlings and 2-year-olds combined.

The means and ranges of the numbers of fringed tapeworms screened from specimens of different sex and age groups are shown in Table 18.

Table 17.

Incidence* of fringed tapeworms (*Thysanosoma actinooides*) in intestinal samples† from wapiti collected in the research series in Banff and Kootenay National Parks and the Ya Ha Tinda Ranch, 1961 to 1965

Period of collection	Age and sex of wapiti							All ages, both sexes
	1 year		2 years		≥3 years			
	♂	♀	♂	♀	♂	♀		
June	-	-	1/2	1/1	0/1	0/2	2/6	
July	-	-	2/2	2/2	1/1	0/1	5/6	
August	2/2	2/2	-	-	0/1	-	4/5	
September	2/2	2/2	0/2	0/1	0/5	0/4	4/16	
October	2/4	0/2	1/1	-	0/5	1/4	4/16	
November	-	1/1	-	-	-	0/2	1/3	
December	3/3	0/1	-	0/1	0/2	0/1	3/8	
February	1/1	-	0/2	1/2	0/1	0/1	2/7	
March, April	0/2	0/1	0/1	-	-	0/3	0/7	
May	1/1	0/1	-	-	0/1	0/2	1/5	
All months	11/15	5/10	4/10	4/7	1/17	1/20	26/79	

* Number of specimens contained in

98

* Number of specimens containing tapeworms/number examined.
† Duodenum and anterior 3 m of jejunum.

Table 18. Numbers of fringed tapeworms (*Thysanosoma actinoides*) in intestinal samples* from wapiti collected in the research series in Banff and Kootenay National Parks, and Ya Ha Tinda Ranch, 1961 to 1965

	Age and sex of wapiti					
	1 year		2 years		3 years	
	♂	♀	♂	♀	♂	♀
Average	10.4	6.7	1.6	1.6	0.12	0.10
Range	(0-54)	(0-24)	(0-8)	(0-5)	(0-2)	(0-2)
No. examined	15	10	10	7	17	20

* Duodenum and anterior 3 m of jejunum.

Yearlings had the highest mean number of tapeworms and the highest individual loads whereas wapiti 3 years old and older had the lowest mean number of tapeworms and the lowest individual loads. Evidently the resistance of wapiti to infection with this parasite increases in relation to age.

Of the 254 fringed tapeworms screened from samples, 146 were from the duodenum and 108 from the anterior 3 m of jejunum. There was no indication of seasonal changes in the distribution of tapeworms between those two segments of the intestine.

Although this parasite has been reported to damage the health of domestic sheep by blocking the bile and pancreatic ducts (Mönnig, 1947:101), it has not been observed to cause disease in cervids (Honess and Winter, 1956:123).

Pulmonary Hydatid Cysts (*Echinococcus granulosus*)

In the sylvatic cycle of the tapeworm in North America, the intermediate host is usually a member of the Cervidae and the definitive host is commonly the wolf (Cameron and Webster, 1961). Cameron and Webster noted that in cervids the usual site of infection is the lung. The first record of this parasite from National Parks in the Canadian Rockies was reported by Cowan (1948) who identified hydatid cysts in wapiti in both Jasper and Banff in 1944. Cowan examined one wolf, one cougar and six coyotes (*Canis latrans*) from Jasper and found *E. granulosus* in the wolf only. Holmes (1961) found *E. granulosus* in 2 of 15 coyotes examined from Banff in the winter of 1959-60. As normally developed ova were present in a small proportion of the worms, the results indicated that coyotes could be locally important in maintaining sylvatic echinococcosis.

Opinions have varied concerning the effects of hydatid cysts on the welfare of the host. Cowan (1951) noted that black-tailed and mule deer, and wapiti infected with hydatid cysts were usually impoverished and of low vitality, and considered it almost certain that their ability to survive other adverse circumstances was impaired. However, Rausch (1952) on the basis of examinations of moose reported, "The larvae of *Echinococcus granulosus* appear to be essentially non-pathogenic in their natural mammal hosts." Rausch suggested that because older ungulates had a greater probability of being infected, the tendency of hydatid infections to be associated with poor physical condition of the host could be attributed entirely to the general effects of old age on the host.

The only heavy hydatid infection noted in the research series occurred in a 21-year-old cow examined October 14, 1962. Although the adrenal glands of that animal were relatively large, suggesting that the infection was stressing the host, the kidney fat index (108%) compared favorably with that of others in the series.

In any case, displacement of part of the lung tissue by hydatid cysts can be expected to reduce the capacity of the host for oxygen exchange (Guyton, 1956:457). Writing of hydatid cysts in horses Soulsby (1965) stated, "A marked infection of the lungs may lead to dyspnoea on exercise . . .". Pulmonary hydatid infections can therefore be expected to increase the vulnerability of the hosts to predation by wolves as that usually involves pursuit (Cowan, 1947b; Mech, 1966). Cowan (1947b) found that a substantial proportion of the wapiti killed by wolves in Jasper from 1943 to 1946, were in the "prime" age group, and suggested that the vulnerability of those animals to predation may have resulted from the effects of hydatid infections. Ritcey and Edwards (1958) reported an instance in which a fat

young cow moose with an extremely heavy hydatid infection died in a corral trap when approached by the captors. Mech (1966:144-150) examined two intact carcasses of wolf-killed adult moose, and both carried heavy hydatid infections.

Green (1949) reported incidences of hydatid infections in wapiti slaughtered in Banff in the four winters between 1944 and 1948 as: 1.7%, 6.8%, 6.06%, and 4.9% respectively. In the present study, hydatid cysts were found in the lungs of wapiti from the Bow, Cascade, Panther, and Red Deer valleys in Banff. They were also found in animals slaughtered in Jasper. No hydatid cysts were found in the lungs of 147 wapiti examined during the slaughter in Waterton Lakes in 1958-59, nor in those of six wapiti, all older than calves, collected in Kootenay in 1962.

The incidence of hydatid cysts in the lungs of wapiti taken in the Bow valley, between December, 1958 and November, 1965 is presented in Table 19 according to the sex and age of the hosts. Similar data from animals taken in the Cascade and Red Deer drainages during the same period are presented in Table 20, and from animals taken in Jasper in 1963-64, in Table 21. Data for a composite sample made up of the above three samples are presented in Table 22. In the sample from the Cascade and Red Deer drainages there was a significant difference between the incidence of infection of males as compared to that of females in the group 6 to 9 years old and in all animals older than yearlings. However, there were no significant differences between incidences of infection in males as compared to females from either of the other areas or from the composite sample. The incidence of infection did not increase consistently with increases in age in any of the samples. There are a number of factors which may have influenced the incidence of hydatid infections in wapiti of

Table 19. Incidence of pulmonary hydatid infections in wapiti
examined in the Bow Valley, Banff National Park, 1958
to 1965

Age in years	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
< 1	0	83	0	71	0	154
1	4	75	4	67	4	142
2	17	41	18	89	18	130
3-5	23	93	29	172	27	265
6-9	18	61	18	121	18	182
≥ 10	29	14	24	62	25	76
≥ 2	20	209	23	444	22	653

Table 20. Incidence of pulmonary hydatid infections in wapiti
examined in the Cascade and Red Deer drainages, Banff
National Park and the Ya Ha Tinda Ranch, 1960 to 1965

Age in years	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
< 1	0	24	0	24	0	48
1	0	26	0	22	0	48
2	7	13	11	28	10	41
3-5	10	20	6	49	7	69
6-9	0	15	28	64	23	79
≥ 10	0	4	24	50	22	54
≥ 2	6	52	19	191	16	243

Table 21. Incidence of pulmonary hydatid infections in wapiti
examined in Jasper National Park, December, 1963 and
January, 1964

Age in years	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
< 1	0	8	5	19	4	27
1	12	16	6	16	6	32
2	0	5	5	21	4	26
3-5	7	15	11	44	10	59
6-9	11	9	18	38	17	47
≥ 10	100	2	40	5	57	7
≥ 2	13	31	14	108	14	139

Table 22. Incidence of pulmonary hydatid infections in wapiti
examined in Banff and Jasper National Parks and the
Ya Ha Tinda Ranch

Age in years	Males		Females		Both sexes	
	Infected (%)	No. examined	Infected (%)	No. examined	Infected (%)	No. examined
< 1	0	115	1	114	0	229
1	4	117	4	105	4	222
2	14	59	14	138	14	197
3-5	19	128	22	265	21	393
6-9	14	85	21	223	19	308
≥ 10	30	20	25	117	24	137
≥ 2	17	292	21	743	20	1035

different sex and age, and in different areas. They are: variations in the abundance of wolves and coyotes, the distribution of wapiti of different sex and age in relation to the distribution of the canids, age-related resistance to infection, and mortality selective for infected wapiti. With the data available the effects of these factors cannot be separated. Since the incidence of hydatid infections in males is similar to that in females, (Table 22) the data do not indicate that hydatid infections contributed to the mortality of one sex more than the other.

Thread Lung-worm (*Dictyocaulus viviparus*)

This parasite has a direct life cycle. The eggs are coughed out by the host, or swallowed and passed in the faeces. They develop through two larval stages on the ground, and the host is infected by ingesting larvae of the second stage on forage (Chandler, 1955:436).

The incidence of the thread lung-worm is presented in Table 23 for wapiti in the research series, along with specimens examined from the slaughters in Banff from December, 1958 to January, 1966. The animals are grouped according to sex, age, and the month of the year.

When data on all wapiti older than calves are treated together, a seasonal cycle in incidence of infection becomes evident. A peak of incidence was reached in July and August. That was followed by a decline through autumn and winter, and a build-up beginning in May. When the incidence of infections in specimens taken from October to April was compared with that of specimens taken from May to September, the difference was significant ($P < 0.005$). The seasonal cycle of incidence suggests that few if any wapiti became infected during the winter. According to Mönnig (1947) the larvae of *Dictyocaulus filaria* rarely live through the winter in cold climates. *D. viviparus* is probably similar in that respect.

Table 23. Incidence* of thread lung-worms (*Dictyocaulus viviparus*) in wapiti examined from Banff and Kootenay National Parks and the Ya Ha Tinda Ranch, December, 1958 to January, 1966

Period of collection	Age and sex of wapiti									
	Calves		1 year		2 years		>3 years		>1 year, both sexes	
	♂	♀	♂	♀	♂	♀	♂	♀	Ratio	Percentage
June	-	-	-	-	2/2	0/1	0/1	0/2	2/6	33.3
July	-	-	-	-	1/2	2/2	1/1	1/1	5/6	83.3
August	-	-	2/2	2/2	-	-	0/1	-	4/5	80.0
September	-	-	0/2	1/2	0/2	0/1	1/5	1/4	3/16	18.8
October	-	-	0/4	1/2	0/1	-	0/5	0/4	1/16	6.2
November	0/9	0/3	0/3	0/4	1/7	1/12	0/16	2/68	3/110	2.7
December	1/61	0/56	0/52	3/43	0/23	2/51	2/116	2/40	11/525	2.1
January	1/38	0/36	0/35	0/34	0/13	0/53	0/60	1/185	1/380	0.3
February	-	0/1	0/1	-	0/2	0/2	0/1	0/1	0/8	0.0
March and April	-	-	0/2	0/1	0/1	-	-	0/3	0/7	0.0
May	-	-	1/1	1/1	-	-	0/1	0/2	1/5	20.0

* Number of wapiti infected/number examined.

A number of workers have reported frequent and heavy infections of thread lung-worms in wapiti which died in winter (Schwartz and Mitchell, 1945; Banfield, 1949; Cowan, 1951; Honess and Winter, 1956:178). Schwartz and Mitchell, and Banfield described overstocking of wapiti and depletion of forage stands associated with their observations. Similar circumstances probably prevailed in the instances reported by Honess and Winter, and Cowan. Longhurst and Douglas (1953) reported "most infections in winter" for *D. viviparus* in samples of Columbian black-tailed deer collected year-round in northern coastal California. As the range was severely depleted, lowered host resistance no doubt contributed to the high winter infections in that situation, and also, a milder climate may have permitted the survival of infective larvae on the range in winter.

The data collected in the present study (Table 23) were from wapiti populations on generally moderately stocked ranges in satisfactory condition. Evidently under those circumstances most wapiti were successful at ridding themselves in autumn of the lung-worm loads which they acquired during the previous summer. This interpretation is consistent with findings of Barrett and Worley (1966) which indicated that the incidence and average worm burden of *Dictyocaulus* sp. in wapiti in winter tended to vary directly with the previous and current use of the range. The data presented in Table 23 do not suggest any differences in incidence of lung-worm infection in relation to sex or age of wapiti. That is in agreement with the findings of McBee, Worley, and Barrett (cited by Barrett and Worley, 1966).

Biting Louse (*Damalinia concavifrons*)

Lice of the above species were found on 8 neck samples and 10

chest samples from 12 wapiti of 51 collected from September through June and of which skin samples were examined (Appendix 8). Samples from only one animal, specimen 83, carried more than 23 lice. That was a very emaciated cow (almost 19 years old) collected in May, and the sample taken from only one side of the chest carried 459 lice. The neck sample was free of lice.

Biting lice of mammals subsist on bits of hair, skin scales, and dried blood from scabs. They cause considerable irritation and, when abundant, weaken the host and make it more susceptible to other diseases (Metcalf, Flint, and Metcalf, 1951:916). Cowan (1951) noted that *Damalinia* spp. tended to be more numerous on hosts in poor physical condition, and the condition of specimen 83 in the present study conforms to this relationship.

Winter Tick (*Dermacentor albipictus*)

The winter tick first attaches itself to the host in autumn or winter as a larva, engorges three times with two moults, without leaving the host, and in spring as an adult drops to the ground where the female lays her eggs (Cowan, 1951; Gregson, 1956).

Winter ticks were found on wapiti from all areas of collection represented in the research series, and occurred in one or more life stages on skin samples of 34 of 45 wapiti examined that were taken during the period October 1 to June 30. From September and July only six and one skin samples respectively were processed, and none of them carried ticks.

Mean numbers of ticks per sample are summarized according to sex and age group of the host, life stage of the tick, and month of collection in Appendix 9. Specimens from which the skin sample was

Table 24. Average number of ticks (*Dermacentor albipictus*) on skin samples* of wapiti 16 months old and older collected in Banff and Kootenay National Parks and the Ya Ha Tinda Ranch, 1961 and 1962

Period of collection	Stage of ticks				No. wapiti sampled
	Larvae	Nymphs	Adults	All stages	
September	0	0	0	0	6
October	6	10	0	16	14
December	0	677	14	691	10
February	0	194	138	332	5
March, April	33	40	266	339	6
May, June	0	1	1	2	10
July	0	0	0	0	1

*December samples consisted of collar 25 cm wide immediately posterior to ears. Other samples included collar plus rectangle 25 cm by 12.5 cm, taken from each side of chest.

the following information is required:

(b) (4)(i)

the following information is required:

the following information is required:

Name	Address				City
	Street	City	State	Zip	
1	100	100	100	100	100
2	200	200	200	200	200
3	300	300	300	300	300
4	400	400	400	400	400
5	500	500	500	500	500
6	600	600	600	600	600
7	700	700	700	700	700
8	800	800	800	800	800
9	900	900	900	900	900
10	1000	1000	1000	1000	1000

The following information is required:

from only one side of the animal are so noted in Appendix 8, and in the computations on which Appendix 9 and Table 24 are based, the numbers of ticks found on those samples were multiplied by two. The samples are too small for the data on numbers of ticks presented in Appendix 9 to be suited to statistical analyses. Although there was great individual variation in tick load, inspection of the data does not suggest differences in the numbers of ticks infecting wapiti of different sex and age groups.

When the data on mean numbers of ticks of each life stage per sample from wapiti of both sexes and all ages are consolidated (Table 24), the phenology of the three life stages of the ticks is indicated. Larval ticks first appeared in October. The only wapiti from a later month on which larval ticks were found was one taken in April that was carrying 200, the largest number of that stage found on a sample from a single host. Nymphs were present on some specimens in each period from October through June, but reached peak numbers in December. Adults first appeared in December samples, reached a peak in March and April, and occurred in small numbers on some May and June specimens. No samples from January or November were examined. The observations on the seasonal distribution of the life stages of the winter tick are consistent with Gregson's (1956) discussion of the life cycle of this species. He noted that the larvae are very tolerant of snow and low temperature and unless brushed onto a host may remain on the ends of grass and twigs until spring.

The incidences of ticks on the skin samples studied are given according to sex and age of the host and period of the year in Appendix 10. In Table 25 the data from different months are consolidated. The

Table 25. Incidence* of ticks (*Dermacentor albipictus*) of all stages on skin samples† of wapiti collected in Banff and Kootenay National Parks and the Ya Ha Tinda Ranch, October through June, 1961 and 1962

Sex of host	Age of host			Total
	16-24 months	28-36 months	>40 months	
Male	12/12	3/4	8/10	23/26
Female	4/6	2/3	5/10	11/19

* Number of specimens carrying ticks/number sampled.

† December samples consisted of collar, 25 cm wide immediately posterior to ears. Other samples included collar plus rectangle 25 cm by 12.5 cm, taken from each side of chest.

It is assumed that the material is homogeneous and isotropic. The material is assumed to be elastic and the deformation is assumed to be small. The material is assumed to be in a state of equilibrium and the forces are assumed to be conservative. The material is assumed to be in a state of equilibrium and the forces are assumed to be conservative.

Table 1. Material properties				
Material	Young's Modulus (GPa)	Poisson's Ratio	Density (kg/m³)	Thermal Expansion Coefficient (1/K)
Steel	210	0.3	7850	12
Aluminum	70	0.33	2700	23

The material properties are assumed to be constant and the material is assumed to be in a state of equilibrium. The material is assumed to be in a state of equilibrium and the forces are assumed to be conservative. The material is assumed to be in a state of equilibrium and the forces are assumed to be conservative.

only sex-age group in which all the wapiti studied carried ticks was the males 16 to 25 months old, represented by 12 animals. The lowest incidence was in adult females, of which five of ten were infected. Samples from individual sex-age groups were too small for meaningful statistical comparison. Data from males of all ages were therefore compared with data for all ages of females. Among 26 males taken from October through June, 23 were infested with ticks whereas among 19 females taken during the same period, only 11 carried ticks. The difference was significant.

Trager (1939) demonstrated that infestation of guinea pigs and rabbits with larvae of *Dermacentor variabilis* or *D. andersoni* induced an immunity which prevented the engorgement of larvae to which they were later exposed. The immunity took the form of an intense inflammatory reaction in which a layer of leucocytes and thickened epithelium walled off the tick from its food supply so that it usually died. Similarly, resistance by some horses and cattle to attachment by *D. albipictus*, "appears to be due to an ability to form scabs at the point of attachment thus healing the wound and throwing off the tick with the scab" (U.S. Department of Agriculture, 1965:58).

It is not known what factors might cause male wapiti to have a higher incidence of infection than females. Perhaps males have a lower resistance to the attachment and survival of ticks. That could be related to the lower fat reserves of males in winter. On the other hand the use of different habitats, or more travel on the part of males might increase the probability of contact with tick larvae.

Cowan (1951) considered the winter tick one of the most serious parasites of big game mammals in Western Canada. Honess and Winter (1956)

reported evidence that heavy tick loads caused hemoglobin depletion and extreme weakness in wapiti calves on artificial feeding grounds. They pointed out that the engorgement of adult female ticks takes place from mid-winter until spring, a period when the host is already in its poorest condition.

Published observations of dead or dying wapiti carrying heavy infections of winter ticks seem mostly to have been made under circumstances in which the host population was dense and the range depleted (Banfield, 1949; Love, 1955; Murie, 1951:166). Peterson (1955:185) similarly noted that the heaviest tick infestations reported in moose in Canada were coincident with high population levels.

The data from the present study show that a large proportion of a wapiti population can contract substantial loads of winter ticks under conditions of moderate stocking on a range in satisfactory condition. While tick infections are probably seldom the sole cause of mortality they could combine with other adverse circumstances to cause mortality. A sex difference in the incidence of tick infections such as is indicated here could cause higher late winter mortality among males than among females.

ADRENAL GLANDS

Selye (1950) has pointed out that a wide variety of agents that upset the homeostasis of a mammal stimulate similar physiological responses of the body. He termed such agents, stressor agents, and the responses of the body, the general adaptation syndrome. He demonstrated that increased secretion of ACTH (adrenocorticotrophic hormone) by the anterior pituitary and the resulting increased secretion of steroid hormones by the adrenal cortex are important features of the response of the body to the effects of stressor agents.

Selye (1950) divided the general adaptation syndrome into three stages: the alarm reaction, the stage of resistance, and the stage of exhaustion. He defined the alarm reaction as the sum of all non-specific, systemic phenomena elicited by the sudden exposure to stimuli that affect large portions of the body, and to which the organism is quantitatively or qualitatively not adapted. Some of those phenomena consist of damage to the organism. Others, which include increased secretion of corticoids and hypertrophy of the cells of the adrenal cortex are manifestations of active defense against damage and they become apparent very soon after the application of the stress. During the latter part of this stage resistance to stresses in general usually is increased.

The stage of resistance is the sum of all non-specific, systemic reactions elicited by prolonged exposure to stimuli to which the organism has acquired adaptation. It is characterized by an increased resistance to the particular stressor to which the body has been exposed, often accompanied by a marked decrease in resistance to other types of stress. This stage is characterized by both hypertrophy and hyperplasia of the adrenal cortex.

The stage of exhaustion represents the sum of all non-specific, systemic reactions that ultimately develop as the result of very prolonged exposure to stimuli to which adaptation has been developed but could no longer be maintained. In this stage abnormal function of the anterior pituitary - adrenal cortex relationship causes an upset in general metabolism.

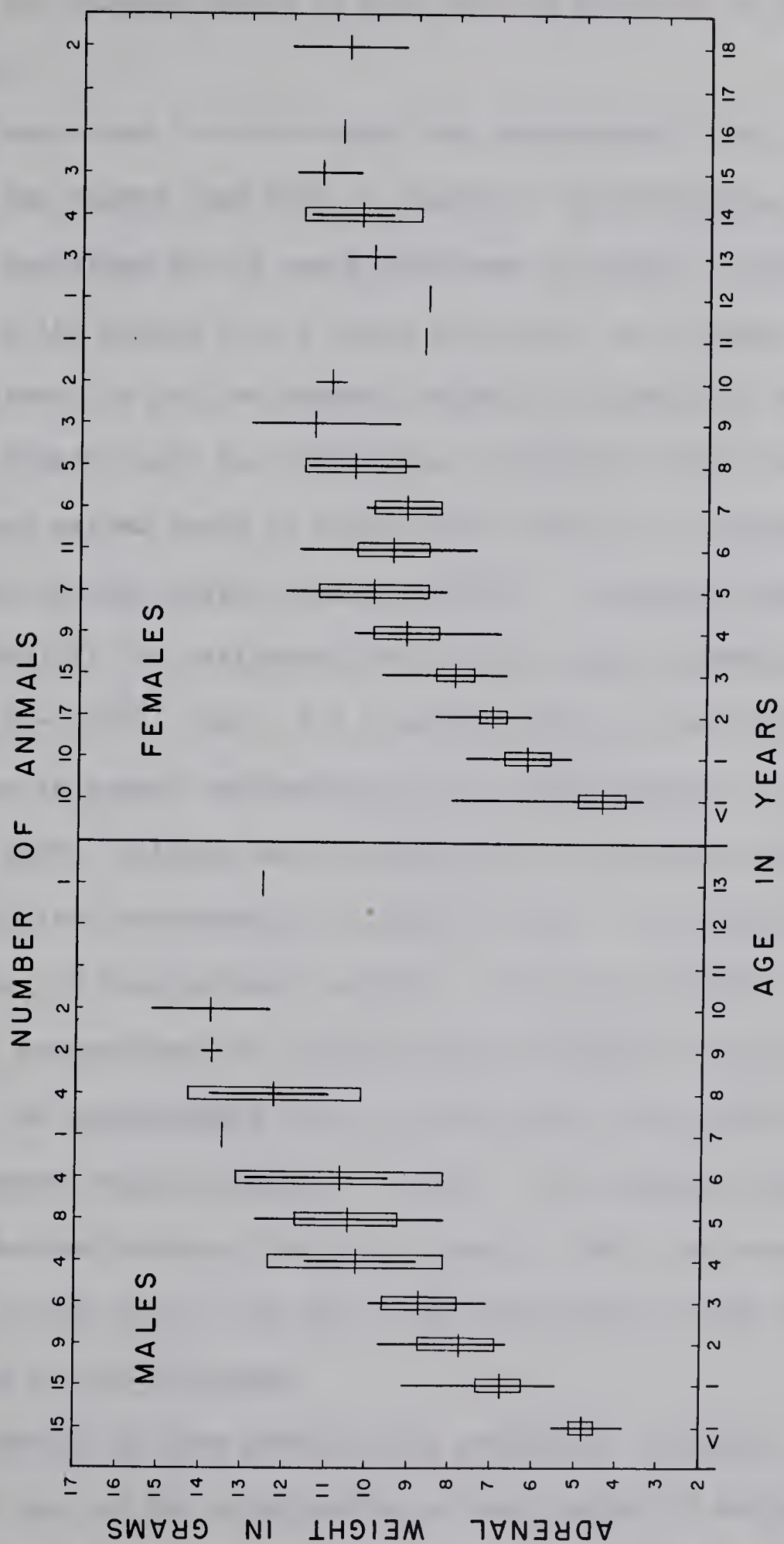
In a number of eutherian species in which the relative weights of the adrenal medulla and cortex have been measured, the cortex makes up the majority of the total weight. The size of the medulla in contrast to that of the cortex is relatively stable (Jones, 1957:11; Selye, 1950:300). Therefore, the weight of the adrenal glands provides a suitable indicator of changes in the size of the cortex. Stress stimulates secretion of ACTH. That usually causes adrenal enlargement, a widening of the zona fasciculata, and a narrowing of the zona glomerulosa (Jones, 1957:28,237).

Difference in Adrenal Size Associated with Sex and Age

In order to provide material for comparing the sizes of adrenal glands according to sex and age, adrenals were collected from wapiti slaughtered in Banff in 1961-62 and 1962-63. They were preserved in neutralized saline formaldehyde solution. Later the glands were trimmed of remaining fat, blotted lightly, and weighed to the nearest 0.01 g.

The 7-year-old males and the 5-year-old females were the youngest classes in which the mean adrenal weights were not significantly smaller than the means of all older animals of their respective sexes (Fig. 18). Thus, the adrenals apparently continued to grow for 2 years in males and 1 year in females, on the average, after full body weight was attained. The graph suggested that adrenal weight might have continued to increase to 10 years old in males and 8 years old in females, 3 years and 1 year older respectively than the corresponding ages for body weight.

Fig. 18. Weight of adrenals of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.





Preliminary data published by Taber, White, and Smith (1959) suggested a tendency for the adrenal weight of mule deer to continue to increase in advanced age.

In each age class in which males were represented, their mean adrenal weight was higher than that of females. The difference was not significant in yearlings but it was significant in calves, 2-year-olds, 3-year-olds, and the groups 4 to 6 years old, and 7 to 13 years old.

In an attempt to put the adrenal weights of animals of different body size on a common basis for comparison, an adrenal weight ratio was derived. Adrenal weight tends to relate more closely to surface area of the body than to body weight (Jones, 1957:6). A general formula given by Spector (1956:175) for estimating the surface area of mammals from body weight is $K = A/W^{2/3}$ where K = a constant for the particular species, A = surface area in square centimeters, and W = body weight in grams.

Kleiber (1965) pointed out the obstacles to measuring surface area and interpreting its relationship to metabolic rate. He reported that, for a large group of homiothermic species, the basal metabolic rate was on the average, proportional to the body weight raised to approximately the $3/4$ power. He acknowledged that for individual species the most appropriate exponent varied somewhat from $3/4$. The European Association for Animal Production accepted Kleiber's proposal that they adopt the term, "metabolic body size," and that it be equivalent to body weight in kilograms raised to the $3/4$ power.

In the absence of data specifically applicable to wapiti on either basal metabolic rate or the relationship of body weight to surface area, metabolic body sizes of wapiti slaughtered in Banff in 1961-62 and 1962-63 were estimated as body weight in kilograms raised to the $3/4$ power. For

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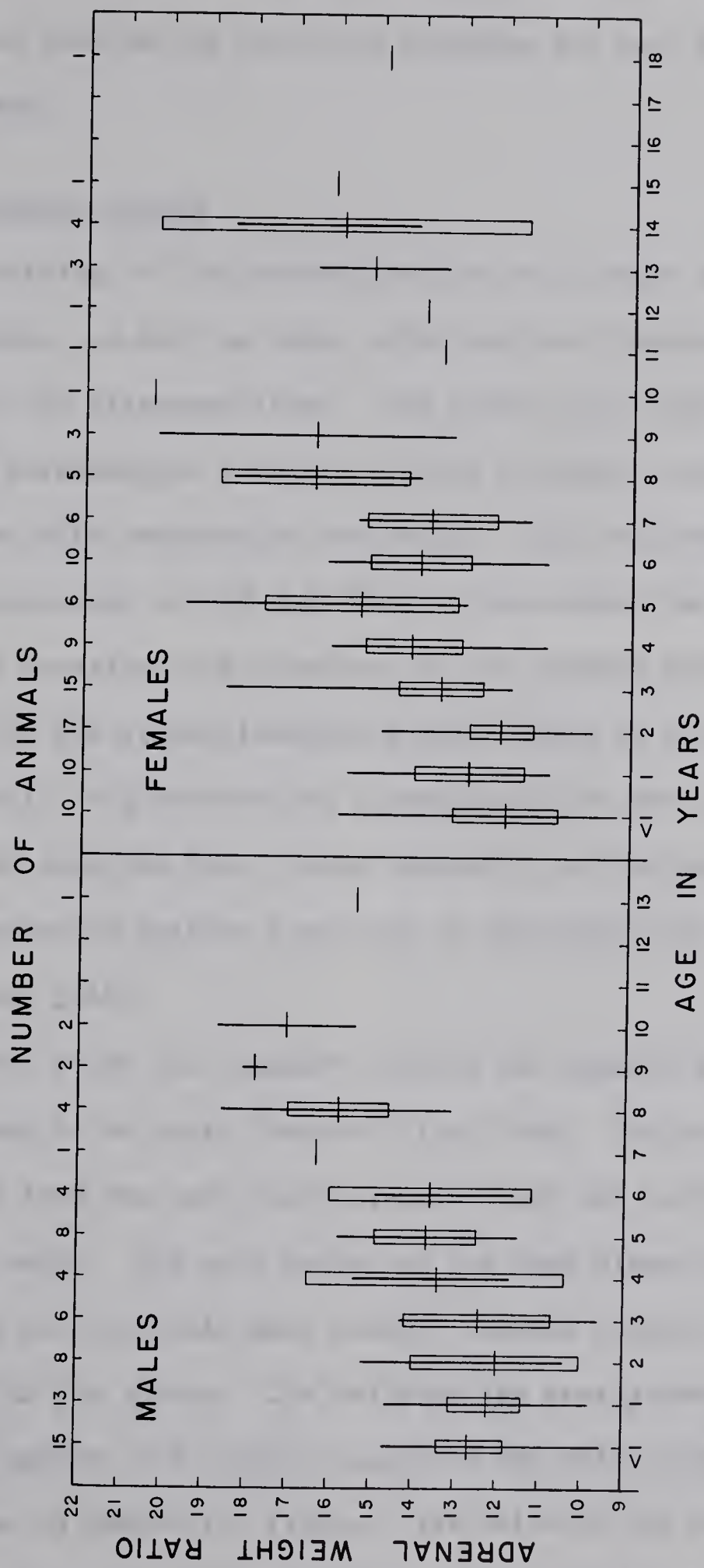
each animal an adrenal weight ratio was calculated by dividing the weight of the paired adrenals in grams by the estimate of metabolic body size, and multiplying the quotient by 100 to make the ratio a whole number.

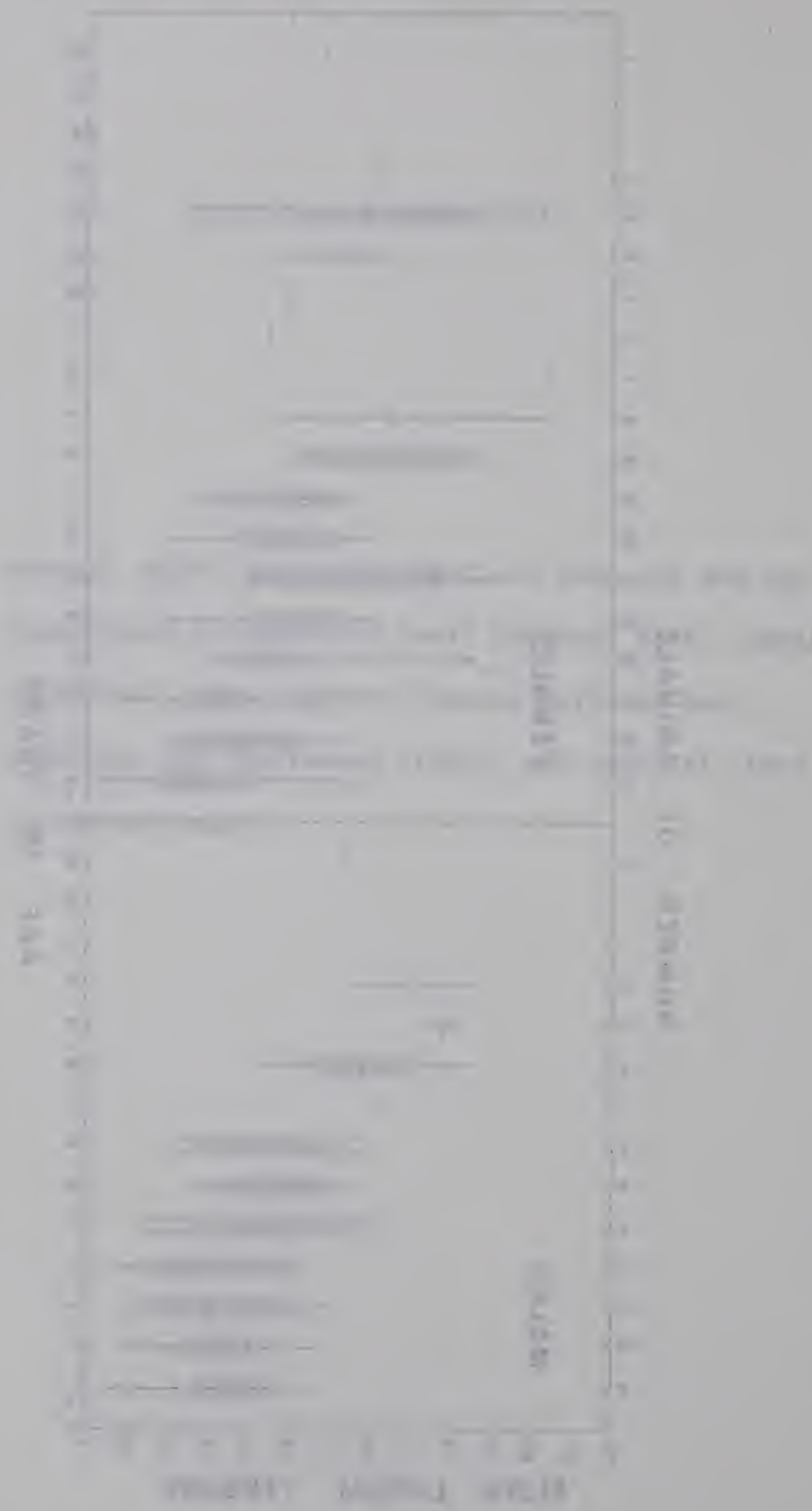
The above treatment of the adrenal weight data reduced some of the variation associated with age (Fig. 19). In the males there were no significant differences among the adrenal ratios of calves, yearlings, 2-year-olds, and 3-year-olds. Similarly in the females there were no significant differences among calves, yearlings and 2-year-olds. However in adults of each sex, the adrenal weight ratio tended to increase in a step pattern in relation to age. In males there were significant differences between the mean ratios of the calf-to-3-year-old group and the 4-6-year-old group, and between those of the 4-to-6-year-old group and the 7-13-year-old group ($P < 0.01$). In females there were significant differences between the mean ratios of the calf-to-2-year-old group and the 3-to-7-year-old group ($P < 0.01$) and between those of the groups 3 to 7 years old and 8 to 18 years old. The increase in adrenal weight ratio with age, as well as the previously described increase in absolute adrenal weight both suggest an increase in the demands for corticoid hormones in relation to age, in addition to the increase related to body size.

The spread of confidence limits (Figs. 18 and 19) relative to their respective means suggest that within each sex-age class the variability of the adrenal weight ratio was similar to that of the adrenal weight.

Most or all of the variation in adrenal weight associated with sex was compensated for by dividing it by metabolic body size. There were no significant differences between the mean adrenal weight ratios of males

Fig. 19. Adrenal weight ratios of wapiti of each sex and age slaughtered in winter in Banff National Park. Median horizontal lines represent means, vertical bars represent 95% confidence limits, and vertical lines represent ranges.





and females in each of the age groups: calves-to-3-year-olds, 4-to-6-year-olds, and 7-years-and older. That similarity suggests that the demands of males and females for corticoid hormones are very similar in relation to body size.

Histology of the Adrenal Cortex

The gross histology of the adrenal cortex was studied in specimens in the research series, as well as those which had been exposed to various stressors to be discussed later. The glands were fixed in neutralized saline formaldehyde solution. After weighing, sections were prepared and stained with hematoxylin and eosin. They were examined under a compound microscope at 40X and 100X to distinguish the zones.

Hucin (1957) described the histology of the adrenal cortex of red deer. Apart from the proportionately greater width of the zones of the gland in wapiti, his description is applicable to the latter species as well. He used the term, "zona arcuata", for the zona glomerulosa as a number of authors have done in describing the adrenals of ungulates (Bourne, 1949).

In the present study the boundary between the capsule and the zona glomerulosa was found to be quite distinct (Fig. 20A). The zona glomerulosa was distinguishable from the zona fasciculata by both the configuration and arrangement of cells. The cell nuclei of the zona glomerulosa were more darkly stained and the cells more tightly crowded together than those of the inner zones of the cortex. The cells of the zona glomerulosa were arranged in loops, arches, and columns usually a few cells wide, separated by radial trabeculae of connective tissue. The cells of the zona fasciculata were arranged in crooked radial strings usually one cell wide. In specimens in which the zona glomerulosa was of small or moderate width,

Fig. 20. Photomicrographs of adrenals of wapiti. H and E stain.

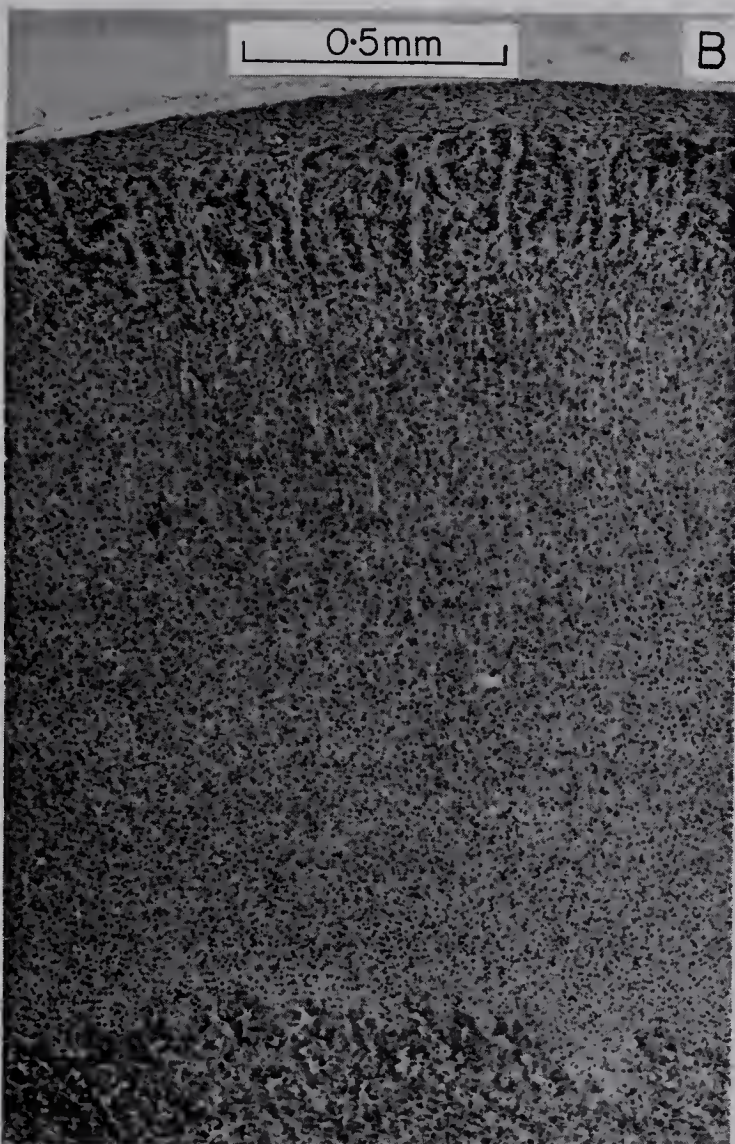
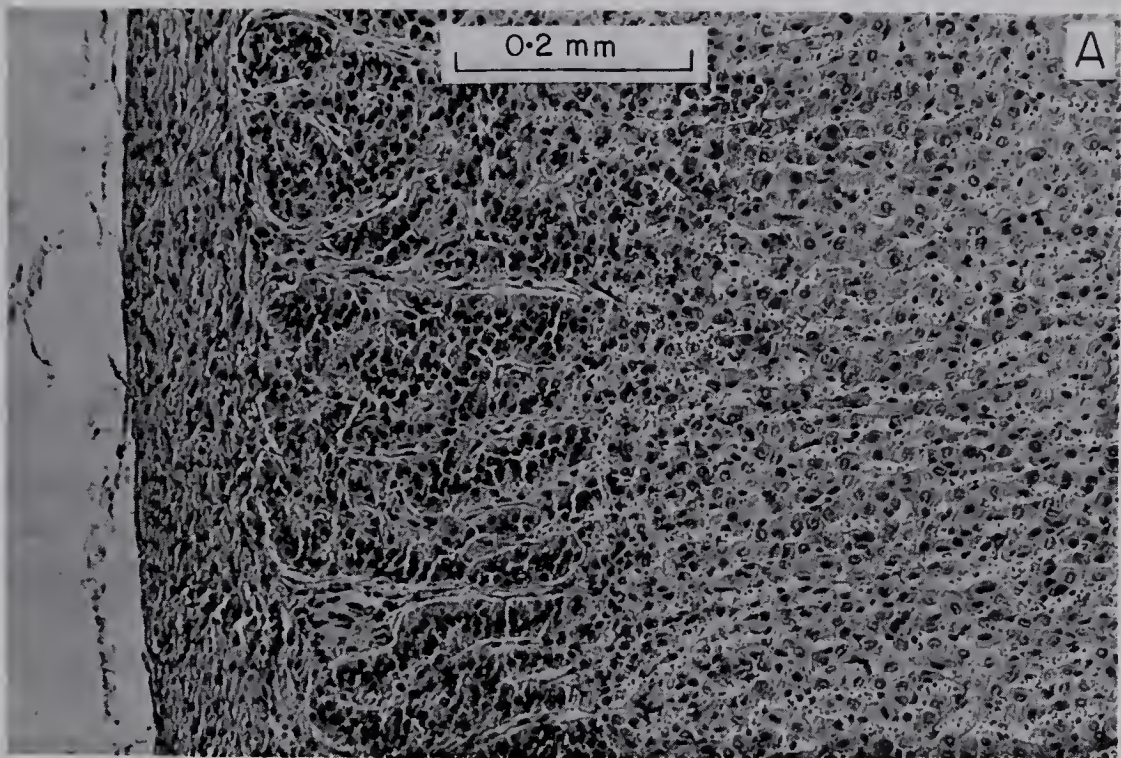
A. #76, female, 9 years old, March 30, 1962, Ya Ha Tinda Ranch.

Left to right: capsule, zona glomerulosa, zona fasciculata.

B. #76. Top to bottom: capsule, zona glomerulosa, zonae fasciculata/reticularis, medulla.

C. #86, male, 6 years old, June 1, 1962. Banff National Park.

Note wider zona glomerulosa, narrower zonae fasciculata/reticularis, and wider transition between them.





the boundary between it and the zona fasciculata tended to be fairly distinct (Fig. 20B). However in specimens with wide glomerular zones the staining characteristics and arrangement of the cells graded less abruptly into the zona fasciculata (Fig. 20C). In specimens of the latter type the boundary was considered as the line where characteristics were approximately intermediate between those typical of the two zones. Towards the medulla, the cell columns typical of the zona fasciculata became disorganized in the zona reticularis. Between the zone of clearly fascicular arrangement of cells and that of reticular arrangement there was a zone of gradation which within a gland varied considerably in width and in proximity to the zona glomerulosa and to the medulla. Hucin (1957) noted that in red deer the transition from the zone fasciculata to the zona reticularis often is not very distinct. Hoffman and Robinson (1966) stated that in white-tailed deer normally only two major zones can be easily distinguished, the zona glomerulosa and the "zonae fasciculata/reticularis", and they did not attempt to divide the latter further.

Only the width of the zona glomerulosa was measured in the present study. To make measurements an ocular disc micrometer was used at a magnification of 100X. It was considered desirable to ascertain the magnitude of variation in width of the zona glomerulosa as measured in the right and left adrenal of the same wapiti, and at different locations in the same gland. The adrenals of specimen 30, a 2-year-old female collected November 27, 1961 were used for that purpose. Four transverse sections were taken at equal intervals along the length of the left gland, and three sections were taken from the right. In this wapiti and in most the right gland was shorter than the left.

In each section, the width of the zona glomerulosa was measured at eight points, four distributed at about equal intervals on each of the two flattened sides of the gland. The width of the zona glomerulosa, represented by the mean of the eight measurements was determined for each section (Table 26). Since the measurements were very uniform, one transverse section from the center of each adrenal was used for measuring the zona glomerulosa and eight measurements were taken from it in the manner described above. Zona glomerulosa widths presented hereafter represent, in most cases, the mean of 16 measurements, 8 from each adrenal gland. In the few instances in which only one usable gland was available, the mean represents eight measurements from that gland.

Effects of Stressors on the Adrenals

In order to help interpret data on the adrenal measurements of wapiti, the adrenals of animals which were known to have been subjected to certain stressor agents, i.e., accelerated loss of body heat, bacterial and parasite infections, and malnutrition were studied. These were all mentioned by Selye (1950:27-51) as agents which can elicit the general adaptation syndrome.

In an attempt to ascertain the effects of accelerated loss of body heat on the adrenals, six wapiti were captured from Banff and Yoho in November, 1961 by immobilization with succinylcholine chloride (Flook *et al.*, 1962) and released in a large, partly wooded enclosure which contained good stands of native forage. Unfortunately four escaped from the enclosure and only one was recovered. Thus, experimental data were available from only the following three animals: a 2-year-old male captured in Yoho Park on November 25, and a male calf in Banff on November 21. Immediately after capture and prior to release in the enclosure, the hair was shorn

Table 26. Width of zona glomerulosa in cross sections from different locations in the adrenals of wapiti 30, a 2-year-old female

	Section	Mean* width of zona glomerulosa (mm)
Left adrenal	1	0.51
	2	.54
	3	.53
	4	.51
Right adrenal	1	.51
	2	.50
	3	.52

* Mean of eight measurements

from a rectangular area from immediately posterior to the shoulder to the base of the tail, and extending on each side of the mid-dorsal line a distance equal to one-sixth the chest girth. Another 2-year-old male was captured in Banff on November 24, and released in the enclosure without treatment as a control animal. The calf was among those which escaped from the enclosure, but it was shot December 5, thirteen days after shearing. The two bulls were shot December 19 which was 24 and 25 days after their release in the enclosure.

During the 24 day interval between shearing and slaughter of the 2-year-old bull the mean daily minimum, mean daily mean and mean daily maximum temperatures were 1° , 9° and 19°F respectively. Corresponding values for the 13 day interval between clipping and slaughter of the calf were 4° , 15° , and 28°F . For both periods the extreme low was -29°F .

On butchering, it was found that the control animal had contracted a *Staphylococcus** infection in the hip puncture inflicted by the projectile syringe used to administer the immobilizing drug. Therefore, that animal was subjected to stress, and the results were interpreted accordingly. The shorn 2-year-old carried five liver flukes. No other endoparasites were observed in any of the animals.

The body weight losses and kidney fat indices of the three animals are presented in Table 27. All three lost a high proportion of body weight during the experiment. At the end of the experiment all three had relatively low kidney fat indices but none had exhausted the fat deposits surrounding the kidneys. The animal with the *Staphylococcus* infection lost the highest proportion of its body weight and had the lowest kidney fat index.

* Identified by Canada Department of Agriculture, Veterinary Research Laboratory, Lethbridge, Alberta.

Table 27. Body weight losses and kidney fat indices of three male wapiti stressed experimentally in November and December

Age (yr)	Treatment	<u>Body weight</u>		Kidney fat index (%)
		Initial (kg)	Loss (%)	
2	<i>Staphylococcus</i> abscess	281	15.6	28
2	shearing	272	11.7	37
<1	shearing	176	9.5	47

As specimen 102, a 21-year-old cow collected October 14, 1962 in the Cascade River Valley (Appendix 7) carried an extremely heavy pulmonary infection of hydatid cysts; it too will be included in the present analysis.

A. L. Lovaas of the Montana State Game Department supplied data and useable adrenals from eight wapiti that died under conditions of extreme emaciation between March 4 and April 4, 1962 in the Gallatin Canyon, Montana. The forage stands of that area were badly depleted as a result of many years of overstocking with wapiti in winter (Peek, Lovaas, and Rouse, 1967). Lovaas (pers commun) reported that the femur marrow was of gelatinous consistency. In 8 specimens it was red, in one calf it was grey. According to Riney's (1955) findings on the relationship of the consistency and color of femur marrow to its fat content, those specimens would have had very little marrow fat. It seems reasonable to assume that malnutrition was the primary cause of death of the Gallatin specimens and data on their adrenals will be interpreted accordingly.

The adrenal weights and zona glomerulosa widths of all specimens known to have been exposed to stressor agents were compared with the mean values of animals of the same sex and age group in the slaughter series or the part of the research series collected at the appropriate time of year. Table 28 includes all the comparisons except that for a group of six female calves from the Gallatin. Since it is the only group involving more than a single specimen exposed to a stressor, statistics for it are included separately in Table 29.

Animals exposed to stressor agents (Tables 28 and 29) did not exhibit a consistent response in either adrenal enlargement or reduction in

Table 28. Adrenal measurements of stressed wapiti compared to those of normal wapiti

Individual stressed specimen				Standard for comparison					
Stressor	Month of death	Sex	Age (yr)	Adrenal measurement	Sample	Mean	Range	Standard error	No.
Heart loss	December	♂	<1	zg width(10^{-1} mm)	-	-	-	-	-
			2	adrenal wt (g)	SS ♂♂ 2 yr	7.8	6.6-9.7	0.37	9
				zg width(10^{-1} mm)	RS ♂♂ 2 yr Dec-April	4.4	3.4-5.2	0.31	6
Abscess	December	♂	2	adrenal wt (g)	SS ♂♂ 2 yr	7.8	6.6-9.7	0.37	9
				zg width(10^{-1} mm)	RS ♂♂ 2 yr Dec-April	4.4	3.4-5.2	0.31	6
Hydatid cysts	October	♀	21	adrenal wt (g)	SS ♀♀ >5 yr	10.1	8.4-12.9	0.56	52
				zg width(10^{-1} mm)	RS ♀♀ >3 yr May-Nov	5.6	3.7-7.6	0.30	15
Malnutrition	March	♂	1	adrenal wt (g)	SS ♂♂ 1 yr	6.8	5.4-9.1	0.25	15
				zg width(10^{-1} mm)	RS ♂♂ 1 yr Dec-April	5.0	4.3-7.1	0.33	8
		♀	10	adrenal wt (g)	SS ♀♀ >5 yr	10.1	8.4-12.9	0.56	52
				zg width(10^{-1} mm)	RS ♀♀ >3 yr Dec-April	4.4	3.0-5.6	0.31	8

zg - zona glomerulosa

SS - Slaughter Series

RS - Research Series

None of differences between measurements of stressed specimens and normal samples were significant at 0.05 level of probability by "t" test.

Table 29. Adrenal measurements of female wapiti calves which died of malnutrition in Gallatin Valley, Montana in March and April, compared to those of female calves slaughtered, Banff National Park, November to January

Cause of death	Adrenal weight (g)				Zona glomerulosa width (10^{-1} mm)			
	Standard			No.	Standard			No.
	Mean	Range	error		Mean	Range	error	
Malnutrition	4.50	3.6-5.1	0.349	4	2.97	2.8-3.5	0.341	6
Slaughtered	4.46	3.5-8.1	0.736	10	-	-	-	-

zona glomerulosa width. Using Student's *t* test (Simpson *et al.*, 1960: 176,182) none of the adrenal measurements of animals exposed to stress were found significantly different from those of normal animals. The adrenal weight of the cold-exposed 2-year-old male and the aged cow with the heavy hydatid infection were each approximately equal to the highest extreme in the most appropriate control group as shown in Table 28. The adrenal weight of each of the other specimens exposed to stressor agents was well within the range of extremes of its control group. It seems particularly noteworthy that the mean adrenal weight of the four calves which died of malnutrition was about equal to the mean adrenal weight of their control group, and the individual adrenal weights of each of the two older specimens which died of malnutrition was well within the range of extremes of its control group.

The zona glomerulosa widths of all the specimens which died of malnutrition tended to be small. However, no data on the zona glomerulosa width of normal wapiti calves in March and April were available for comparison. Zona glomerulosa width of none of the other specimens exposed to stressors differed appreciably from the mean of its corresponding control group.

It was attempted to determine whether infections with each of the 5 parasites commonly noted in the study: winter ticks, giant liver flukes, hydatid cysts, fringed tapeworms, and thread lung-worms, even though they were not heavy, were associated with an increased adrenal size or decreased width of the zona glomerulosa. Within each sex and age category in the research series, the individual and mean values of adrenal weight and thickness of zona glomerulosa of wapiti infected with each parasite were compared with those of specimens not infected with that particular species (Appendices

6 to 8). In cases where inspection of the data suggested the possibility of a real difference, Student's t test was applied. None of the individual or mean zona glomerulosa widths of parasitized animals was significantly smaller than that of the non-parasitized group of the same age and sex. Similarly none of the individual or mean adrenal weights of parasitized specimens was significantly larger than that of the non-parasitized group of the same sex and age. When the adrenal measurements of specimens carrying two or more species of parasites were inspected and compared with mean and individual measurements of others in their sex-age groups, no consistent differences from the norm were noted. The number of animals infected with each parasite was small and the parasite loads generally light. However larger samples of animals as heavily parasitized as specimen 102 might be found to exhibit detectable differences in either adrenal size or zone widths when compared to non-parasitized samples.

The literature contains the results of a number of experiments conducted to study the effects of stressful treatments on the activity of the adrenal glands in various mammals. Munday (1961) showed that laboratory rats exposed to 0° to 2°C for 48 hours exhibited increased sodium retention and potassium excretion, mediated by the adrenal, and concluded that increased secretion of mineralocorticoids was involved. Rats exposed to that temperature for 28 days had a significantly greater adrenal weight than control animals, and rats exposed to cold for several weeks showed hypertrophy of the cortex and an increase in width of the zona fasciculata. In contrast, Griffiths, Callaby, and McIntosh (1960) found no detectable effects of cold on wild rabbits exposed to 0°C . Rabbits of reasonably uniform body size collected from the field showed marked variation in adrenal weight, both absolute and relative to body weight. Rabbits exposed to -12°

to -15°C for 6 to 7 hours daily for 20 days and then held at that temperature for 3 days without food or water, showed a mean relative adrenal weight only slightly higher than that of control animals, and the difference was not significant. Rabbits injected with dilute formaldehyde over a 7-day period, and killed 18 days later after 15-18 hours of cold exposure, exhibited marked adrenal hypertrophy. Noise-adapted rabbits exhibited increased resistance to cold stress, but rabbits which previously had been injected with formaldehyde and apparently resisted it, were unable to resist cold stress. Griffiths *et al.* concluded that in wild rabbits, both histological change and hypertrophy of the adrenal cortex are exhibited only under much more severe stress than that required to induce such effects in laboratory mammals.

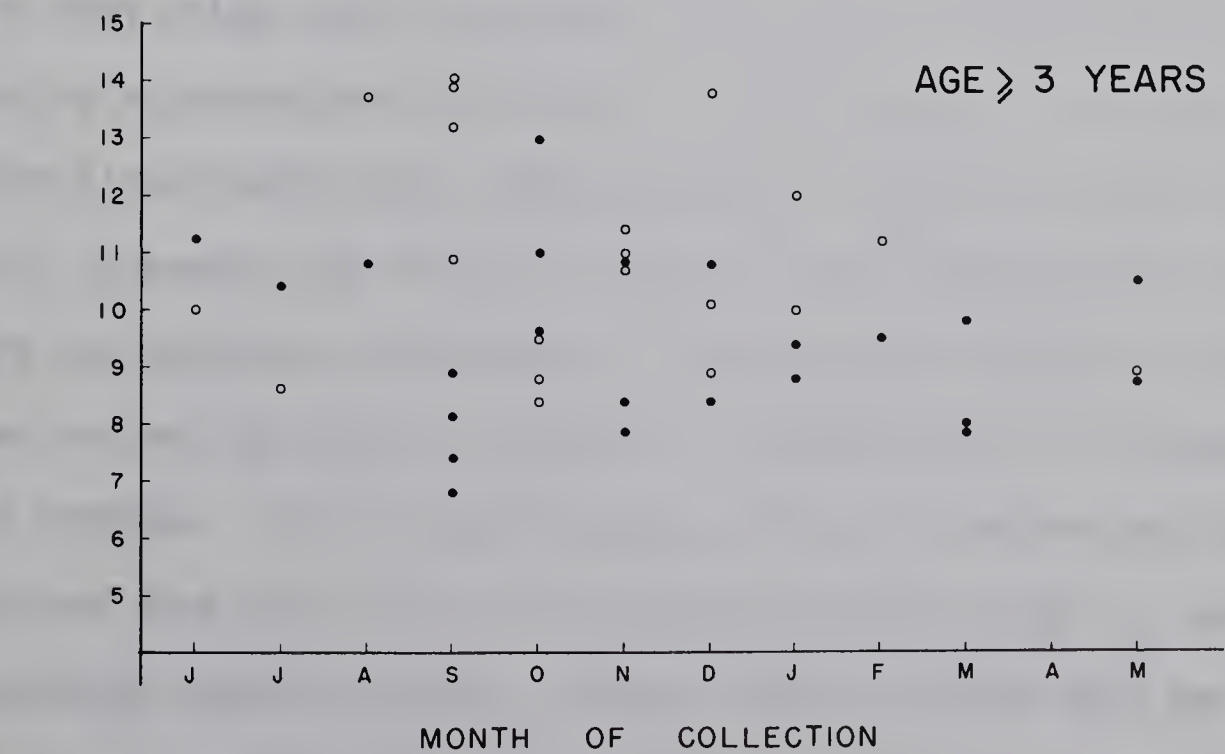
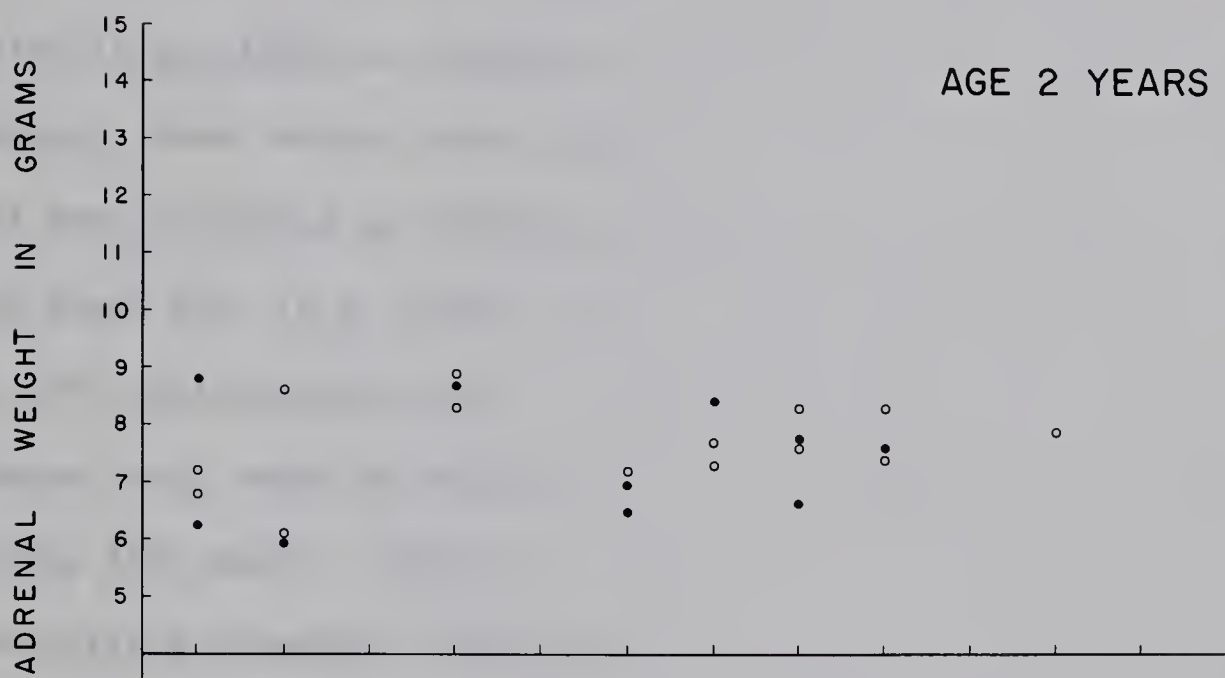
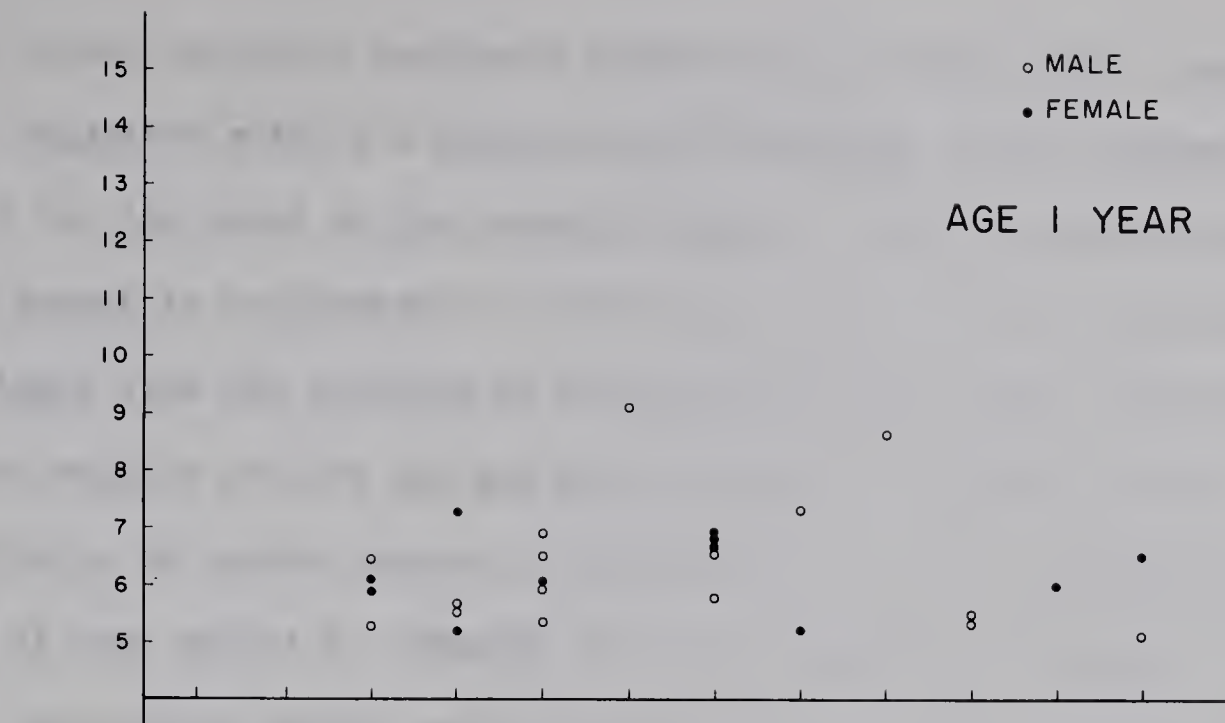
The literature contains evidence that adverse circumstances can cause adrenal enlargement in cervids. Hughes and Mall (1958) found a significant negative correlation between adrenal weight and kidney fat deposits in adult female Columbian black-tailed deer. Bubenik and Bubenik (in press) compared the adrenal weight relative to dressed carcass weight of roe-deer (*Capreolus capreolus*) from a population living at low densities in favorable habitat with comparable data from a population living at high densities in less favorable habitat. They divided the samples from each population according to sex, age, and physical condition, the latter rated by size of body and antlers, fat deposits, disease, parasites and injuries. Relative adrenal weight tended to be greater in samples from the dense population and in animals in poorest condition. The trends in absolute adrenal weight calculated by the present writer from the data given, were in the same direction, but were less pronounced and less consistent.

Christian, Flyger, and Davis (1960) reported that adrenal enlargement was associated with a late winter die-off in a dense, insular population of sika deer (*Cervus nippon*) and concluded that the die-off was caused by physiological disturbances induced by sociopsychological pressures related to crowding. Their adrenal data were based on 4 specimens collected during the die-off and a total of 13 collected 3 and 1 year prior to, and 1 and 2 years after the die-off. They used relative adrenal weights (adrenal weight/body weight) in their comparisons. However body weights of the four specimens collected during the die-off were the lowest for their sex-age classes. The absolute adrenal weights of the four deer collected during the die-off, calculated by the present writer from their data, differ less markedly from those of the pre- and post-die-off specimens than is the case in the relative adrenal weights. The range of variation in adrenal weight noted in the present study (Fig. 18) suggests that, if sika deer are similar to wapiti in this respect, variation in adrenal weight of the magnitude noted by Christian *et al.* between specimens taken during the die-off, as compared to those taken prior to, and after it, could be encountered under normal circumstances.

Seasonal Changes in the Adrenals

Weights of the adrenals of wapiti in the research series are presented in Fig. 21, with the animals distinguished as to age group and sex. As was noted for wapiti taken in the slaughters, the adrenal weights showed great individual variation. The data suggest a peak in adrenal weight in adult males in August and September. However, since the single high August value, the three high September values, and the single high December value all represent specimens 7 years old or older, and 11 of the

Fig. 21. Weights of adrenals of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch.



14 lower values represent specimens younger than 7 years old, it appears that the suggested peak is a function of differences in age (Appendix 6). Similarly the low level of the adrenal weights of the four adult females taken in August is attributable to their ages which are all less than 6 years. Apart from the features of the data mentioned above, the distribution of adrenal weights of each sex-age group suggest no seasonal trend.

A ratio of adrenal weight to body weight, or to an exponential function of body weight is commonly used for comparative purposes (Jones, 1955:6). An adrenal weight ratio was used in the present study to compare adrenal size in specimens of different sex and age taken from November to early January. Some workers have used such an index to compare adrenal weights of deer collected at different seasons, and with markedly different amounts of depot fat (e.g. Taber, *et al.*, 1959, mule deer: Hoffman and Robinson, 1966, white-tailed deer), or collected under other differing circumstances which would be expected to influence fat reserves (Christian *et al.*, 1960, sika deer). However, as white fat is a relatively inactive tissue metabolically (Hayward, 1964:55-58), it is not to be expected that a decrease in body weight which represents utilization of depot fat will be accompanied by a proportionate decrease in adrenal size. It has been shown in Columbian black-tailed deer (Hughes and Mall, 1958) and roe-deer (Bubenik and Bubenik, in press) that lower fat reserves and correspondingly lower body weight are sometimes accompanied by larger adrenal weight in animals of the same sex and age group, presumably a manifestation of the general adaptation syndrome. In the present study, while fat reserves and body weight declined from early winter to spring (Appendices 6 and 7), adrenal weight apparently remained stable. However samples of deer with low fat reserves and correspondingly low body weights, even though their adrenals are

not enlarged, have a higher ratio of adrenal weight to body weight than do fat deer simply because the index is a function of body weight. Indices based on the relationship of adrenal weight to body weight are therefore useful only in comparing samples in which the fat deposits relative to body size are reasonably similar.

Hoffman and Robinson (1966) who studied white-tailed deer in a crowded population in Maryland, reported two seasonal peaks in adrenal weight relative to body weight, one in November and December, and one in March and April. Bimonthly mean absolute adrenal weights calculated from their data show only a single annual peak in November and December. This contrasts with the apparent seasonal stability in adrenal weight indicated here for wapiti.

Zona glomerulosa widths for the research series are presented in Fig. 22, with the specimens distinguished as to age groups and sex. The widths exhibit great variation even between animals of the same age and sex and collected in the same month. However, they suggest a seasonal trend, widest in the period from June until September and narrowest from December to April. Figure 20, A and B illustrate the adrenal cortices of specimens with one of the smallest and the largest zona glomerulosa widths observed, respectively. Within each of the six sex-age groups studied, the zona glomerulosa width was compared between specimens collected from May through November and those collected from December through April (Table 30). The differences were significant in each group except yearling males. No yearlings were collected in June and July, the months when the older animals showed their greatest zona glomerulosa widths. Had the yearling males been represented in collections made in those months they too might have shown a significant difference between summer and winter. As the total size of the

Fig. 22. Zona glomerulosa widths of individual wapiti older than calves, according to sex, age, and month of collection, Banff and Kootenay National Parks and the Ya Ha Tinda Ranch.

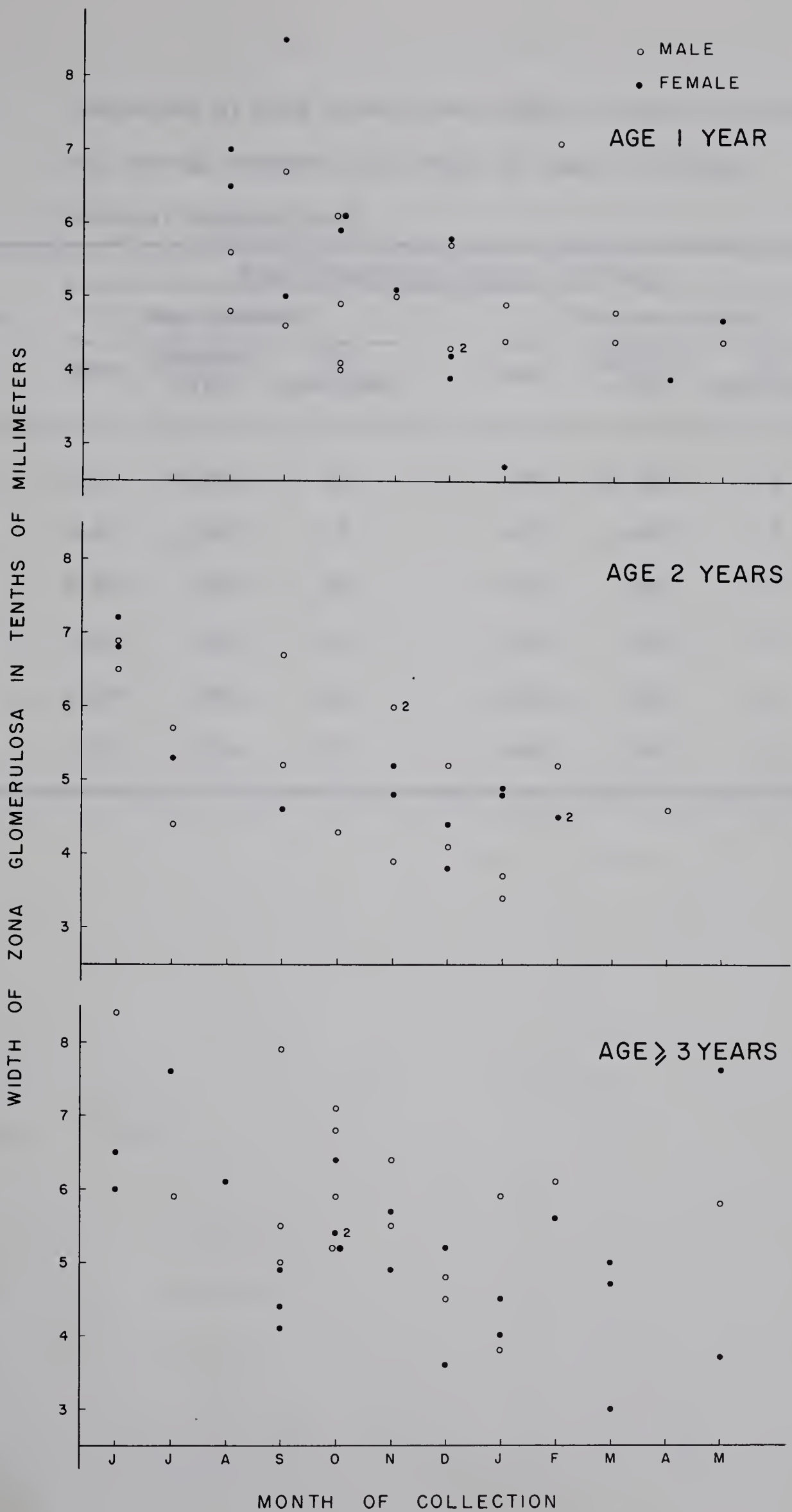


Table 30. Comparison of zona glomerulosa widths of wapiti collected May through November with those of wapiti collected December through April

Age (yr)	Sex	Zona glomerulosa width (10^{-1} mm)					
		May-November			December-April		
		Mean	Standard error	No. specimens	Mean	Standard error	No. specimens
1	♂	5.02	0.275	10	4.98	0.334	8
	♀	6.10	.442	8	4.10	.497	5
2	♂	5.56	.334	10	4.36	.310	6
	♀	5.65	.442	6	4.48	.158	6
≥3	♂	6.28	.309	12	5.02	.433	5
	♀	5.59	.296	15	4.45	.307	8

adrenal gland appears not to have changed in relation to season, the reduction in zona glomerulosa width in winter indicates an increase in the size of the zonae fasciculata/reticularis.

The seasonal trend in zona glomerulosa width of wapiti conforms in part to the findings of Hoffman and Robinson (1966) whose data showed that in white-tailed deer the smallest bimonthly mean zona glomerulosa width for the year occurred in January and February. However, in wapiti, there was no evidence of a second decrease in July and August such as was suggested by the data of Hoffman and Robinson.

The few specimens in the present study which were known to have been exposed to accelerated heat loss, infection, or malnutrition did not respond consistently in either adrenal enlargement or reduction of the zona glomerulosa. The adrenals of two specimens, one cold stressed, and one infected with hydatid cysts were relatively large, but the zona glomerulosa widths were normal. On the other hand, the zona glomerulosa widths of the specimens which died of malnutrition were relatively small but the adrenal weights were normal. Jones (1957:237) reported that stimulation by ACTH caused the zona glomerulosa to decrease in width in rats and dogs, and when ACTH stimulation caused a 50% increase in the adrenal weight of rats, the zona glomerulosa disappeared. Controlled experiments with cervids are needed to explain the significance of the seasonal difference in zona glomerulosa width indicated by the present study. A tentative interpretation is that it can be attributed to the stressful effects of low temperatures, snow accumulation, and less bountiful food supplies in winter. While the level of ACTH secretion was evidently high enough in winter to cause the zona glomerulosa to be partly replaced by zonae fasciculata/reticularis, the adrenal weight data (Fig. 21) show

that it did not cause an increase in the total size of the gland. It is noteworthy that while the zona glomerulosa width decreased simultaneously with a winter decline in fat reserves (Fig. 15), it increased earlier in the spring.

Neither the data on adrenal weights nor zona glomerulosa widths suggested that in wapiti one year old or older, males were subjected to more severe stress than females.

POPULATION DYNAMICS

Data on the numbers of animals of each age and sex, removed by the National Parks Service for population control, supplemented by the results of a few segregated counts of living wapiti will be used, to examine the population dynamics of wapiti in the parks.

Appendices 11 to 14 list the numbers of wapiti removed each year from Elk Island, Jasper, Banff, and Waterton Lakes respectively, prior to the more detailed data collecting which commenced in the winters of 1957-58 in Banff and Jasper and 1958-59 in Elk Island and Waterton Lakes. In the data from Banff and Waterton Lakes, animals are classified as to sex and two age categories: calves, and those older than calves. Early data from Elk Island cover the period beginning March 1, 1947, the earliest date since which records are complete. In that park some removals were made by trapping live wapiti for transport and some by shooting, and the method for each removal is indicated in Appendix 11. Henceforth the term shooting will refer to shooting free-ranging animals, and trapping will refer to capturing them in corrals baited with hay. Of the latter animals some were removed from the park alive and others were butchered. Data on removals from the other parks include all animals recorded from the time the parks were established until the start of this study. All such removals were accomplished by shooting.

The numbers of wapiti of each sex and year class removed each year during the study from Elk Island, Jasper, Banff, and Waterton Lakes, are presented in Appendices 15 to 19. The methods of removal and whether or not intentional selection was practiced are indicated. In Waterton Lakes, animals were taken by trapping and shooting, but they were not distinguished in the records. Because the population in the Red Deer and Cascade drainages

in Banff is believed fairly discrete from that in the Bow Valley, the data for animals removed from those two areas are presented separately.

Numbers of Wapiti of Each Sex Produced in Elk Island

Certain circumstances make the wapiti population of Elk Island particularly useful for studying population dynamics of the species. That population is enclosed by a fence in an area of 50 square miles, to and from which there is no ingress or egress. The population has been controlled by periodic removals for which records are available for a period of 19 years. An estimate of population size and sex ratio based on ground observations is available for the start of that period, and the results of a total segregated count are available for the close of the period.

In the slaughters in Elk Island prior to December, 1958, shooting of calves was avoided as much as possible, and few were taken in that way. However, the wapiti removed by capture (Appendix 11) included calves in whatever proportion they entered the traps with the cows. Prior to 1958, the slaughter quotas were apparently set so as to keep females in the majority. From December, 1958 until the time of writing, all removals from Elk Island were accomplished by slaughters in which the shooters were instructed to take animals without selection as to sex and age.

The total numbers of wapiti of each sex removed from Elk Island between March, 1947 and January, 1966, along with estimates of the numbers of animals of each sex present at the start and finish of that period, are shown in Table 31. The 1947 estimate was recorded by the late Dr. B. I. Love, Park Superintendent, on the basis of a ground count by the park wardens.

Table 31. Net population change, total harvest, and net production of wapiti of each sex, Elk Island National Park, March, 1947 to January, 1966

Sex	Population estimates		Net decrease 1947 - 1966	Total harvest 1947 - 1966	Net production* 1947 - 1966
	March 1947	January 1966			
♂	254	132	-122	1091	969
♀	304	143	-161	1350	1189
Total	558	275	-283	2462†	2179†

* Total harvest minus net decrease.

† Includes 21 harvested animals of unspecified sex.

The 1966 estimate was obtained from an attempted complete count made by aircraft in January 20 of that year. A Helio Courier fixed-wing aircraft was flown systematically back and forth across the park on east-west lines at one-quarter mile intervals, at a height of about 300 feet and at speeds between 65 and 80 miles per hour. Two observers, one of whom surveyed from each side of the aircraft from the rear windows recorded the species, number, and location of all wapiti, moose, bison and deer (*Odocoileus* spp.) seen, on maps on which the flight lines had been previously drawn. A navigator seated beside the pilot assisted him in following the flight lines. The lines corresponded to the legal divisions of lands adjacent to the park, and at the start of each the pilot oriented his course from road allowances and fence lines. Most of the observers' attention was directed to searching for animals on a strip within one-eighth mile on each side, but many animals were seen farther out, particularly in open habitat. When such animals were sighted on the return flight along the adjacent line, they could be recognized because their location was already plotted on the map. A few animals were seen by different observers from lines one-half mile apart, but such duplications were eliminated after the survey, when locations of animals plotted by the two observers were compared. Single wapiti, and those in small groups, were designated as calves, yearling males (spike antlers), males older than yearlings (branched antlers), and females older than calves. However, as animals could be viewed only briefly while flying the strips, cows, calves, and yearlings in groups of six or more were recorded only as to number and location, and an additional procedure was followed to classify them. The writer met the observers from the Helio Courier when that aircraft returned to Edmonton to fuel, after the northern

two-thirds of the enclosure had been surveyed. The location and number of animals in each group of unclassified wapiti was transcribed to a new map, and the writer proceeded immediately to the park as a passenger in a Bell 47B helicopter. Each group so mapped was located and the members identified as to the sex and age category.

The maximum interval between the time when a group was initially observed in the strip survey, and when its numbers were categorized from the helicopter was six hours. Each group was found near the location where it was initially sighted, and was recognized by the number of animals in it. Animals that were scattered among the aspen trees were gathered and herded into an opening where they were more readily identified and counted. The pilot flew slowly behind and to the left of each larger group, gradually coming along side of it so that the observer, in the righthand seat, could view the animals in profile. In the second flight of the strip survey which covered the southern one-third of the enclosure, the only large groups encountered included only bulls and the observers in the Helio Courier succeeded in classifying all wapiti seen. In arriving at the estimate of numbers of wapiti of each sex present (Table 31), the sex ratio of the 34 calves was assumed to be 1:1.

It will be helpful here to adopt the term net production to signify the absolute number of wapiti harvested during a given period plus the population increase or minus the population decrease during the same period. From 1947 until 1966, 2,462 wapiti were harvested from Elk Island and the population apparently declined by 283 animals to give a net production of 2,179 wapiti (Table 31). If 21 wapiti of unknown sex harvested are disregarded, the net production would have included 969 males and 1,189 females. If it is assumed that an equal number of males and females were

born during the period, then 220 more males than females must have been lost to non-harvest mortality. The sex ratio in the net production was 85:100 and was significantly different from a ratio of 1:1.

The possibility that the higher non-harvest loss of males, as compared to females, was the result of the effects of harvests on the composition of the population, should be considered. If rates of non-harvest mortality of the sexes were equal at equal ages, but males were harvested at lower rates (as a proportion of those living) than females, then a greater number of males would have reached old age, when death from natural causes must be expected. In order for that to have occurred, there should have been more males in the population at most times during the 19-year period. The following evidence indicates that such was not the case.

The park superintendent estimated that there were fewer males than females in the population in 1947. The composition of a sample comprising 64% of the population shot without deliberate selection, November, 1959 to January, 1960 (Appendix 15), indicated that among the animals 3 years of age and older in the population, males were in a minority. Finally, in spite of each slaughter since December, 1958 having removed more females than males, the aerial census in January, 1966 showed fewer males than females among the animals older than calves. Therefore it is concluded that the sex difference in non-harvest losses was not caused by the harvests having allowed more males than females to reach a common age of senility. Rather, a greater proportion of males than females must have been lost to non-harvest mortality within certain age classes.

It is relevant to consider the rates of productivity and harvest of the population during the period in which production of males and females

were compared. To examine these aspects of the population, the period was divided into two parts: March, 1947 to February, 1960; and February, 1960 to January, 1966. This is appropriate because of the following circumstances. From November, 1959 until January, 1960, 410 wapiti and 141 moose were slaughtered in Elk Island. On February 26, 1960 an aerial census carried out in the same manner as that of January 20, 1966, but without identification of animals as to sex and age, resulted in counts of 233 wapiti and 83 moose. Sprouts of aspen, previously suppressed for many years by heavy use by wapiti and moose, responded to the reduction in browsing pressure with a marked increase in height, and throughout the remainder of the study period continued to encroach on grassed openings. Thus the chronological division above separates a period of low densities and a period of high densities.

Leopold (1933:22) defined productivity as, "the rate at which mature breeding stock produces other mature breeding stock, or mature removable crop," and stated that it, "differs from rate of increase in that it includes increments to the removable crop as well as to the breeding stock." Leopold later (1933:171) omitted the word, "mature" from the definition of productivity and also stated, "The unit of productivity, where the increase is removed, is the ratio or percent which can be removed yearly without diminishing the capital." Robinette (1956:415) applied Leopold's latter definition to the term net productivity. Net annual productivity rate will be used in that context in the following discussion, and animals of both sexes and all ages will be treated together in the population base, the harvested segments, and the population increases and decreases.

For the rate of increase of a population, Kelker (1947) derived

the equation, $P = Ar^t$, in which "P" equals the number of animals resulting when an initial population of "A" animals increases at a rate "r" for a period of "t" years. In order to compute the net annual productivity rate of the population in Elk Island Park from the data on the population change and the numbers harvested in different years, Kelker's (1962) equation was expanded as follows:

First, for a situation in which there are two harvests between the initial and final population estimates,

$$P = [(Ar^{t_1}) - H_1]r^{t_2} - H_2]r^{t_3}, \text{ or}$$

$$P = A(r^{t_1+t_2+t_3}) - H_1(r^{t_2+t_3}) - H_2(r^{t_3}), \text{ where}$$

P and A are defined as above,

r = net annual productivity rate,

H_1 = number of animals in first harvest,

H_2 = number of animals in second harvest,

t_1 = number of calving seasons between initial count and first harvest,

t_2 = number of calving seasons between first and second harvest, and

t_3 = number of calving seasons between second harvest and final count.

Then in the general situation,

$$P = Ar^{t_1+t_2+\dots+t_n+t_{n+1}} - H_1r^{t_2+t_3+\dots+t_{n+1}}$$

$$- H_2r^{t_3+t_4+\dots+t_n+t_{n+1}} - H_{n-1}r^{t_n+t_{n+1}} - H_nr^{t_{n+1}}, \text{ where}$$

with the exception that

t_3 = number of calving seasons between second and third harvest,

the above definition of symbols apply, and

H_n = last harvest prior to final count,

t_n = number of calving seasons between next to last harvest and last harvest, and

t_{n+1} = number of calving seasons between last harvest and final count.

In applying the equation for rate of increase Kelker (1947) adjusted the number of males in the initial population so that the sex ratio was 1:1. In the present situation, as the sex ratios at the various stages between the initial and final count were not known, no such adjustments could be made. The computed productivity rate applies to the circumstances that prevailed, and does not represent a potential for the species at a 1:1 sex ratio. It is an average annual value for the period, in the sense that it is based on the assumption that it was constant from year to year, which was of course not so. The equation was applied by substituting three-digit numbers for " r " until the one that most closely balanced the equation was found.

When the equation was applied to the data for the period March, 1947 to February, 1960, a net annual productivity rate of 1.21 or 21% was obtained. However, the 1947 estimate and the 1960 count indicated a decline in the population from 558 to 233. Using the same equation it can be shown that a net annual productivity rate of 22% would have been needed for the population to have sustained the harvests without declining. Because the rates of productivity and harvests would be equal in a stable population, it can be concluded that the harvests over the period March 1947 to February 1960, while they actually varied from year to year, had an effect equivalent to a removal of 22% of the population annually.

When the equation was applied to the data for the period February 1960 to January 1966, a net annual productivity rate of 22% was calculated. The 1960 and 1966 counts showed an increase in the population from 233 to 275. The harvests during that period had an effect equivalent to a removal of 20% of the population annually.

Buechner, Buss, and Bryan (1951) studied a population of wapiti in Washington State by using aerial counts, and numbers killed by hunters over a 6-year period. They computed a "rate of increase" of 24%, using that term in the context that net productivity rate has been used here. They suggested that the numbers counted were probably lower than the actual population, and that therefore the estimated rate of increase was somewhat higher than the actual rate. Murphy (1963) reported a rate of increase of 28% over an 8-year period for a small, enclosed population of wapiti in Missouri. In his computations he evidently adjusted the sex ratio of the wapiti initially stocked in the enclosure, to 1:1.

Distribution of the Sexes, and Classified Counts

In slaughters conducted without deliberate selection, differences in distribution and behavior of the animals associated with age and sex, and subconscious selection by the shooters, could cause samples to be unrepresentative of the populations from which they were taken.

Park wardens in Elk Island consistently reported that during slaughters, most wapiti encountered in the southern part of the main enclosure were bulls older than yearlings, whereas the majority of those in the northern part were cows and followers*. Inspection of the locations of observations from the aerial count of January 20, 1966, showed that the area in which bulls predominated could be separated from that in which cows predominated by an east-west line. The area south of that line, which contained most of the bulls covers 17 square miles and the area

* The term cows and followers is used to designate cows accompanied by calves and yearlings of both sexes.

north, 33 square miles. The numbers of wapiti of each sex-age category, counted in each of those two divisions of the park are given in Table 32, with information on the size and composition of groups counted. In the southern part of the park the trees are smaller and the grassy and shrubby openings more extensive than in the north.

The areas from which wapiti have been removed in the mountain parks have been restricted to those which supported high numbers of wapiti in winter and were accessible by vehicle. They consisted of interspersed grass, shrub, and forest habitats, and with the exception of parts of the Cascade and Red Deer drainages where wapiti were shot early in the winter, are at low elevations and accumulate only a moderate depth of snow. Although some wapiti were present there during the entire year, many were there only in winter and dispersed to higher elevations in summer. In the slaughters there, some bulls were taken in the same general areas as cows and followers but certain localities tended to be more commonly occupied by one or the other of those two categories.

Data on sex-age composition are available from classified counts of wapiti in Banff. In the period October 28 to November 1, 1963, a special survey was conducted by the park wardens. District wardens travelled the valleys of their districts by truck, horseback, and on foot, and with binoculars counted all the wapiti that could be found. When possible they identified them as to one of four categories: yearling males, males older than yearlings, females older than calves, and calves. Each warden also supplied an estimate of the total number of wapiti in his district as based on his survey and his previous experience in the

Table 32. Distribution and grouping of wapiti according to sex and age group, aerial survey of main enclosure of Elk Island National Park, January 20, 1961

Portion of enclosure	Type of group*	Sex, age, and numbers				Group size	
		♂♂ 1 yr.	♂♂ ≥2 yr.	♀♀ ≥1 yr.	♀♀ & ♂♂ <1 yr.	Mean	Range
North (33 sq mi)	Bulls	-	30	-	-	2.7	1-6
	Cows	10	2†	120	33	6.3	1-46
	Total	10	32	120	33	5.3	1-46
South (17 sq mi)	Bulls	2‡	70	-	-	1.7	1-13
	Cows	1	-	6	1	1.6	1-3
	Total	3	70	6	1	1.7	1-13
Entire enclosure (50 sq mi)	Bulls	2	100	-	-	1.9	1-13
	Cows	11	2	126	34	5.6	1-46
	Total	13	102	126	34	3.2	1-46

* Group characterized by most numerous sex among members older than calves.

† Each of the two bulls was a member of a separate cow group.

‡ Two yearling bulls formed a single group.

district. Results of the survey are presented in Table 33.

V. Geist (pers commun), who spent the period May 15 to August 16 in the Cascade Valley studying the behavior of bighorn sheep, recorded all his observations of wapiti, classified as to age and sex. Those observations are presented in Table 34. Geist made no attempt to exclude animals counted on previous days.

In both the survey by park wardens, and the observations made by V. Geist in the Cascade Valley, females strongly outnumbered males among the wapiti older than calves.

Among the wapiti observed in certain habitats in the mountain parks and adjacent areas, bulls have outnumbered cows. In December, 1966 and January, 1967 J. G. Stelfox (unpublished) of the Canadian Wildlife Service conducted a census of bighorn sheep by helicopter in parts of Jasper and Banff known or suspected to support sheep in winter. He also counted all wapiti observed on the high, treeless and sparsely treed slopes and ridges. He identified 49 antlered and 15 antlerless wapiti in Jasper, and 53 antlered and 26 antlerless wapiti in Banff. Most of those were observed in the vicinity of the upper limit of trees. That survey did not cover all potential winter ranges for wapiti at high elevations, and on the ranges surveyed, some animals are thought to have been overlooked among the conifers just below tree-line. Picton (1961) writing of wapiti in Montana described the tendency for bulls to range in small groups at higher elevations and in areas of greater snowfall than cows and calves. After the re-introduction of wapiti in the Bow Valley in Banff in 1918 and 1920, the first reported sighting of wapiti on the Ya Ha Tinda Ranch was in 1933-34 (Cowan, 1944). In 1942-43, 50 to 60 bulls and no cows were reported to be wintering on the ranch (Cowan,

Table 33. Numbers of wapiti of each age group and sex, as counted by park wardens in survey of Banff National Park, October 28 to November 1, 1963

Age (yr)	Sex	Bow Valley	Red Deer and Cascade drainages	Other* areas	Total
<1	♂ & ♀	159	109	96	364
1	♂	36	64	19	119
≥2	♂	83	75	49	207
≥1	♂	119	139	68	326
≥1	♀	291	431	166	888
	ratio				
≥1	♂♂:♀♀	41:100	32:100	41:100	37:100
Unidentified		45	436	71	552
Total count		614	1115	401	2130
Total estimate†		804	1380	495	2679

* Drainages of North Saskatchewan, Clearwater, and Spray rivers.

† Sum of district wardens' population estimates for the districts occupied by wapiti.

Table 34. Numbers of observations of wapiti of each age group and sex in Cascade Valley, Banff National Park, summer, 1963 by V. Geist

Age* (yr)	Sex	May	June	July	August	Total
<1	♂ & ♀	0	39	87	22	148
1	♂	0	28	15	7	50
≥2	♂	37	115	23	12	187
≥1	♂	37	143	38	19	237
≥1	♀	97	221	276	31	625
Unidentified		-	5	2	-	7
≥1	ratio ♂♂:♀♀	38:100	65:100	14:100	61:100	38:100

* Animals observed in May at ages of 11 and 23 months included as 1 and ≥1 year of age respectively.

1944). M. Gilmar, foreman of the ranch for several years, reported (pers commun) that when he first worked there during the winter of 1945, the only wapiti seen were about two dozen adult bulls. He returned to the ranch in October, 1950 and in that winter saw between 80 and 100 cows and followers, but no adult bulls. From then until the time of writing, bulls older than yearlings have rarely been seen on the ranch, but cows and followers have regularly wintered there in large numbers. Some have also ranged in the vicinity in the summer, while others have migrated back up the Red Deer Valley to spend the summer in Banff. When the writer first visited the ranch in 1957, large, bleached shed antlers were still common, attesting to the previous abundance of bulls in the spring.

R. Webb (pers commun), formerly of the Alberta Fish and Wildlife Division, in an aerial survey of wapiti on February 9, 1959 counted 603 cows and followers on the ranch and vicinity, and 21 bulls older than yearlings on the slopes above the ranch. In similar surveys on February 23, 1961; January 9, 1962; and January 26, 1963, Webb counted 516, 685, and 633 wapiti, respectively, on the ranch and vicinity. All were cows and followers.

Harrison Flats is a grass-shrub area on the floor of the Clearwater Valley north of the ranch and east of Banff. Webb first noted wapiti there on his aerial survey of January 9, 1962, when he counted a single herd of 50 adult bulls. On surveying the flats again on January 26, 1963 he observed a herd of 75 adult bulls and a separate group of 4 cows.

The history of wapiti on the Ya Ha Tinda Ranch, and probably also the Harrison Flats area, conforms with Cowan's (1946) comments concerning wapiti in Jasper, ". . . the vanguard of the penetration into new areas

consists of bulls". Writing of red deer, Darling (1956:66) pointed out that typically when new ground is colonized stags are the first to use it. He described an example (1956:51) in which, when hinds took up winter occupancy on a ground that had in previous winters been occupied solely by stags, the latter abandoned it except during the rut. The sequence in which bull wapiti, after pioneering the ranch area, vacated it about the time when cows took up occupancy, parallels the circumstances described by Darling.

Sex and Age Composition of Samples of Wapiti Removed for Population Control

The numbers of wapiti of each sex and age removed from Elk Island during the study, are presented in Table 35. Similar data for removals from each of the three mountain parks: Jasper, Banff, and Waterton Lakes, and a composite of the three, are presented in Table 36, with animals taken in selective removals from Banff (Appendices 17 and 18) excluded. Animals 4 years old and older are treated as one group because data are included from slaughters in which the ages of animals with complete dentition were assigned by tooth wear only, in some cases to broad classes. Table 37 shows the data combined from the mountain parks for those years in which ages were assigned precisely on the basis of cemental layers, with each age class treated separately.

The numbers of yearlings exceeded the numbers of calves among wapiti removed from all parks (Tables 35 and 36), indicating either that calves were under-represented or else yearlings were over-represented.

In order to test the possibility that calves were under-represented in the slaughters, the number of calves and the number of lactating cows in the slaughters were compared. The data available are all from the mountain parks (Table 38). As animals taken in January are included in

Table 35. Numbers of wapiti of each sex and age removed* from Elk Island National Park, December, 1958 to December, 1963

Age (yr)	Males	Females	Ratio males:females
<1	49	70	70:100
1	77	69	112:100
2	61	63	97:100
3	40	78	51:100
≥4	32	181	18:100
?†	27	28	96:100
Total	286	489	58:100
≥2	133	322	41:100

* Shot in winter without deliberate selection.

† Age not known but carcass weight indicated age ≥ 1 yr.

Table 36.

Numbers of wapiti in samples removed* without deliberate selection from Jasper, Banff, and Waterton Lakes National Parks, including samples in which older animals were assigned only to broad age groups, tabulated as to sex and age with animals ≥ 4 years consolidated

Age (yr)	Jasper		Banff				Waterton Lakes				Total	
			Cascade & Red Deer drainages		Bow Valley							
	Dec, '57-Jan, '67	♀	Dec, '60-Dec, '66	♂	Dec, '57-Jan, '64	♀	Nov, '58-Feb, '63	♂	♀	Number	♂	♀
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
<1	21	40	35	33	81	65	32	49	169	187	90:100	
1	48	33	24	21	74	71	64	35	210	160	131:100	
2	16	41	5	26	43	91	23	36	87	194	45:100	
3	19	43	10	23	32	73	12	43	73	182	40:100	
≥ 4	40	167	29	200	150	296	44	134	263	797	33:100	
?†	0	0	5	29	18	17	7	5	30	51	59:100	
Total	144	324	108	332	398	613	182	302	832	1571	53:100	
≥ 2 (no.)	75	251	44	249	225	460	79	213	423	1173	36:100	
≥ 2 (ratio)	26	: 100	18	: 100	49	: 100	32	: 100	36	: 100		

* All animals removed in winter, the majority by shooting, but some in the Cascade and Red Deer drainages, and Waterton Lakes by trapping.

† Age not known. Body size indicated age ≥ 1 year.

Table 37. Numbers of wapiti of each age and sex in samples removed* without deliberate selection from Jasper, Banff, and Waterton Lakes and assigned to yearly age classes

Age (yr)	Males (no.)	Females (no.)	Ratio males:females
<1	96	102	94:100
1	100	85	118:100
2	37	101	37:100
3	40	95	42:100
4	22	69	32:100
5	27	59	46:100
6	20	66	30:100
7	14	53	26:100
8	4	37	11:100
9	12	43	28:100
10	4	28	14:100
11		18	0:100
12	2	14	14:100
13	2	10	20:100
14	2	11	18:100
15		12	0:100
16		7	0:100
17		7	0:100
18		4	0:100
19		2	0:100
Total	382	823	46:100
≥2	186	636	29:100

* Samples removed from Jasper, Dec,'63-Jan,'67; Cascade and Red Deer drainages, Dec,'60-Dec,'66; Bow Valley, Nov,'61-Jan,'64; and Waterton Lakes, Dec,'62-Feb,'63. All animals taken in winter, the majority by shooting, but some from the Cascade and Red Deer drainages and Waterton Lakes by trapping.

Table 38. Numbers of calves and lactating cows taken among wapiti slaughtered* in Jasper, Banff, and Waterton Lakes National Parks

Park	Period of slaughter	Calves	Lactating cows
Jasper	Dec, '63-Jan, '64	28	58
	Nov, '66-Jan, '67	24	41
	Total	52	99
Banff	Nov-Dec, '57	9	16
	Dec, '58-Jan, '59	16	27
	Dec, '59-Jan, '60	44	69
	Dec, '60-Jan, '61	22	42
	Nov, '61-Jan, '62	30	54
	Dec, '62-Jan, '63	48	50
	Dec, '63-Jan, '64	16	18
	Dec, '64-Jan, '65	25	53
	Nov-Dec, '65	1	20
	Nov-Dec, '66	12	21
	Total	223	370
Waterton Lakes	Dec, '62-Feb, '63	23	30
	Total	298	499

* Cows and calves taken without deliberate selection. Most animals taken by shooting, but some in Waterton Lakes and Banff by trapping.

the samples, some of the cows not lactating would have had calves in the population at the start of the slaughter. Therefore, in order for calves and cows to have been represented in the slaughters in the same proportions as were present in the living populations, more calves should have been taken than lactating cows. As the samples contained only 298 calves as compared to 499 lactating cows, it can be concluded that calves were markedly under-represented in the slaughters. The under-representation of calves was probably caused by both a subconscious preference of the shooters for larger targets and an aversion to shooting juveniles.

Females exceeded males in both the sample of calves slaughtered in the mountain parks (90:100) and in the sample slaughtered from 1958 to 1963 in Elk Island (70:100). Only in the latter sample were the numbers significantly different. Most of this difference was contributed by the 1958 slaughter in which 15 female calves and only 2 male calves were taken. By the end of 1963 a total of 53 males and 57 females had been removed in Elk Island from the 1958 year class, as yearlings, 2-year-olds, and five-year-olds (Appendix 15) indicating that the sex ratio of the 1958 calf sample did not represent that of the calves living at that time. There is therefore little reason to conclude that the sex ratio among calves in winter differed substantially from 1:1.

In view of the marked variations in the sex ratio of samples of calves shot in different parks in different years, it is suspected that some sex characteristic causes differences in the vulnerability to shooting, of males relative to females, under different circumstances. Assuming that it was a subconscious preference of the shooters for either larger targets or for adults, that caused calves of both sexes to be under-represented in the slaughters, we might have expected male calves, because of their larger

size, to have been shot in greater numbers than female calves, but that did not occur consistently (Table 36). Although all calves observed during winter were with cows, some subtle behavioral difference may, under certain circumstances, make female calves more likely to be shot. Perhaps they tend to remain near the carcasses of the dams more than male calves. That might affect vulnerability differently in dense cover than in open habitats. Also, if some shooters made greater effort than others to shoot calves remaining after the dam was killed that could cause differences among the sex ratios of calves from different slaughters.

Males exceeded females in both the samples of yearlings slaughtered in the mountain parks (131:100) and in the sample slaughtered from 1958 to 1963 in Elk Island (112:100). Only in the former sample were the numbers significantly different ($P < 0.01$). The shooting of slightly more female calves than male calves may have left more males than females available for shooting as yearlings. However, that effect would have been slight. Because the sex ratio favored females in both calves and 2-year-olds, it seems improbable that there would have been substantially more male than female yearlings in the populations. More likely, some shooters subconsciously selected yearling males. Most yearlings of both sexes are with herds of cows in winter. The distinct appearance of the yearling males may attract attention to them causing them to be shot first.

Andersen (1953) presented data on the age and sex composition of a population of roe-deer at intervals during a period of 2-1/2 months in which it was hunted to extinction. He showed that males were more vulnerable to shooting than females in all age classes.

The relative numbers of wapiti of each sex remaining after 1957 from year classes born in Elk Island prior to that year, may have been strongly

influenced by previous removals having selected for one sex or the other. The composition of samples slaughtered from 1958 to 1963 (Appendix 15 and Table 35) should be viewed accordingly.

The sex ratio of wapiti 2 years old and older slaughtered from the different mountain parks, while it consistently and heavily favors females, varies considerably (Table 36). Earlier data have shown that the winter distribution of bulls is, in part, different from that of cows and followers. In the mountains, more bulls than cows winter on high ranges inaccessible to vehicles. Because slaughtered animals must be salvaged, animals on such ranges are immune to slaughter. Variation among the four mountain areas in the degree to which road access coincides with the winter distribution of bulls is probably a major factor contributing to the variation in the sex ratio of the adults slaughtered. Differences in subconscious selection by shooters, for or against bulls, may also be involved.

In view of the evidence presented previously that males outnumber females on higher winter ranges, and that they tend to pioneer new ranges, the abrupt drop in the male:female ratio at 2 years old in the sample harvested in the mountain parks is thought to be mostly attributable to dispersal of many bulls between their second and third winters from the ranges where they were reared to areas which were not accessible to slaughter.

In the composite sample from the mountain parks the sex ratio remains fairly stable from 2 to about 7 years old, the ratio for the total sample of those six age classes being 36:100. The proportion of males in successive age classes then declines until males become extinct after 14 years of age. Perhaps the mortality rate of males is the same as that of

females between 2 and 7 years old, as the data suggest. However, there is an alternative interpretation. During the rut there appears to be an influx of mature bulls to the lower elevations. Some of the bulls coming from higher ranges may remain at low elevations to replace those that have been slaughtered or lost to natural causes. If this is the case, the mortality rate of bulls younger than 7 years could exceed that of cows of equal age and the result still be consistent with the composition of the slaughtered sample. With the population data available it can be concluded only that the mortality rate of males became higher than that of females sometime after 1-1/2 years of age. The data also strongly suggest that after about 7 years of age the mortality of bulls increased markedly, both as a rate, and relative to that of cows of equal age.

The maximum age of any bulls to which precise age was assigned was 14 years, attained by two specimens taken in slaughters in Banff. The maximum age of cows among those from slaughters was 19 years, also attained by two Banff specimens. One older cow was examined, specimen 102 in the research series, taken in Banff at an age of 21 years. From records of 254 ear-tagged wapiti shot by hunters in Montana, Picton (1961) reported maximum longevities of 12-1/2 years for one bull and 18-1/2 years for two cows.

In addition to the removals of wapiti for population control, two other man-made causes of mortality are collisions with trains and highway vehicles, and recreational hunting on adjacent lands.

Reports by park wardens in Banff and Jasper during the period 1958 - 1965, of wapiti struck by trains and highway vehicles and killed outright or injured so badly that they were shot, are presented in Table 39. The data are not thought to be a complete record of all vehicular deaths, but probably represent fairly the sex and age composition of the total mortality

Table 39. Numbers of wapiti deaths caused by trains and highway vehicles, as reported by park wardens, Banff and Jasper National Parks, 1958 to 1965

	Sex and age of wapiti killed				Total
	♂♂ ≥1 yr	♀♀ ≥1 yr	♂♂ & ♀♀ <1 yr	Not specified	
Train	23	60	12	20	115
Highway vehicle	10	28	16	-	54
Total	33	88	28	20	169

from that cause. The sex ratio of those older than calves was 37:100, the same as that of wapiti counted by park wardens in the survey of Banff in 1963 (Table 33), and of wapiti observed by V. Geist in the Cascade Valley in the same year (Table 34). It supports the other evidence of a disproportionate sex ratio favoring females among adults in the valleys where the highways and railways are located, and indicates that vehicular deaths do not contribute to shifting the sex ratio in that direction. No deaths of wapiti from collisions with vehicles have been reported from Elk Island or Waterton Lakes.

For many years there have been open seasons for wapiti in those parts of Alberta adjacent to Jasper, Banff, and Waterton Lakes. Thus hunting has been a potential mortality agent for any wapiti moving from the parks to occupy those areas during the season when they were legal game.

The Bow Valley east of Banff has for several years been open to hunting of both sexes of wapiti with bow and arrows only, during parts of the months of September through December, but according to W. Wishart of the Alberta Fish and Wildlife Division (pers commun) few animals have been killed. Of 51 wapiti ear-tagged in the Bow Valley inside the park in 1960 and 1961, none have been reported taken outside the park.

Throughout the other wildlife management zones bordering the mountain parks, there has been a season for rifle hunting of bulls only, in parts of September and October, followed by a season for either sex in parts of November and December. Although males have slightly exceeded females in the total harvests from those zones in recent years, females have been in the majority among those taken in November and December, when either sex could be shot (Wishart, 1966, and unpublished). Hunting in the latter season has probably removed more park animals than has the early season,

because the herds which migrate from the parks to winter outside usually do so after the onset of winter weather. Even the late season does not usually result in a harvest of many park animals. Wapiti flushed by shooting during the slaughter operations in the parks have been observed usually to move uphill and into tree cover. Because the parks are located along the continental divide, such movement tends to keep the animals within the parks rather than drive them out. Because wapiti ranges adjacent to the parks are usually at lower elevations, we might expect hunting there to drive any wapiti near the boundaries into the parks. In support of that supposition, since 1959, when hunting was first allowed on the Ya Ha Tinda Ranch, large herds have not become established there until after the season closed. In that year, a special season was opened in January on the ranch and vicinity, and about 200 wapiti were shot.

Occasionally, under conditions of heavy snowfall and winds, wapiti have moved from Waterton Lakes Park to the ranchlands north of the park for short periods. Banfield (1950) reported that about 450 wapiti were shot there in the winter of 1946-67. During the present study, according to observations of park wardens and information obtained by G. Kerr and G. Armstrong of the Alberta Fish and Wildlife Division (pers commun), the numbers killed in that area have been small in spite of hunting of both sexes having been allowed from November until March 15. Those harvests have probably removed the sexes in about the same proportions as have the slaughters inside the park.

Data are not available to assess the proportion of the wapiti born in the mountain parks that are harvested elsewhere. However, the limited information does not suggest that such harvests have been important in altering the sex ratio of the populations surviving in the parks.

DISCUSSION

Although recognized biases in the population data prevented the determination of age-specific mortality rates of males and females, certain conclusions can be reached regarding differences in mortality rates between the sexes and their probable causes.

In Elk Island, apparently more males than females were lost to non-harvest mortality over a 19-year period, but the difference was relatively small. The sex ratio in the net production from Elk Island during that period was 85:100.

The sex ratios of wapiti older than calves in classified counts in Banff, in summer and autumn, and among wapiti killed by trains and highway vehicles in Banff and Jasper at all seasons were between 36:100 and 37:100. The sex ratio of wapiti older than yearlings in a total sample shot without deliberate selection in all the mountain parks in winter (Table 36) was 36:100. However, the apparent disappearance of a large number of males in the mountain parks from the ranges where they were reared, between their second and third winters of life suggests a dispersal. Bulls outnumbered cows in winter at the high elevations and are thought to do so at other seasons as well. One might suspect, because bulls are more solitary than in addition to using the alplands more than cows, they also use small grassy or shrubby openings in the forest more. Thus, the distribution of cows in the mountain parks coincided more closely with accessible areas and perhaps with areas of good visibility than did that of bulls. Therefore population data from the mountain parks obtained by counts and analyses of slaughtered samples are believed to be biased in favor of cows.

The apparent dispersal of young males in the mountain parks to new areas may take some of them into unsuitable habitats and thus actually contribute to mortality of males. Also the wintering of some bulls at higher elevations where the snow is often deeper and the temperatures colder than on the lower ranges, may make them more vulnerable to winter mortality. Males in Elk Island are not exposed to the above potential hazards because the park is fairly uniform in climate, and dispersal from it is prevented by a fence. Greater exploitation by man may also have reduced the effects of natural mortality selective for males in Elk Island as compared to the mountain parks. The above environmental differences between the mountain parks and Elk Island could lead one to hypothesize that the differences in life expectancy between males and females should have been greater in the mountain parks than in Elk Island. However it is not possible to confirm that relationship with the information available because of the bias in the data on sex ratios from the mountains.

The sex ratio of fetuses collected in winter from all parks was 113:100 and differed significantly from equality. Perhaps, as Cowan (1950) suggested, the sex ratio begins at conception to shift from one in which males predominate towards one in which females predominate and continues to do so throughout life. If there were slight changes in the sex ratio during the first 1-1/2 years of life, they could not be detected because of biases in the slaughtered samples. The samples from all parks indicated that no substantial changes took place before 1-1/2 years of age. The suggested dispersal of many males in the mountain parks, from the ranges where they were reared to areas not accessible to slaughter, between their second and third winters of life, made it impossible to determine the age when non-

harvest mortality of males first appreciably exceeded that of females. However, a marked loss of males was indicated beginning after 7 years of age and continuing until 14 years, the age of the oldest males represented. In contrast, the numbers of females declined steadily in successive age classes from 2 to 19 years of age, the maximum age represented in the slaughtered sample.

The data showed that in Banff, Waterton Lakes and Elk Island, males abraded their molariform teeth more rapidly than females, by differences of approximately 9%, 26%, and 40% respectively in the three parks. While the effect of tooth abrasion on health is more probably a gradual rather than a threshold one, it seems likely that it would not have great effect until the more advanced stages. The effects of the progress of tooth abrasion cannot be isolated with the data available, because it is accompanied by general senescence in both sexes, and probably by changes in the participation in breeding by males. It is evident that any effects that tooth wear has on the welfare of wapiti in the three parks mentioned would confer an advantage on females. In the absence of exploitation, when more animals would be given the opportunity to reach older ages, tooth wear could be expected to be more significant in limiting longevity and thus in affecting the sex ratio in those parks. In Jasper, tooth wear, being more rapid than in the other parks, would adversely affect wapiti of both sexes at a younger age. However, it would affect males and females equally at equal ages.

The major features of the life histories of males and females will be briefly summarized and compared. In females body growth continued to an age of about 4 years. Some conceived as yearlings and most did so each year thereafter. The pregnancy rate declined significantly after 13 years of age. However, both of the 19-year-olds examined in winter were pregnant. The

kidney fat deposits of females measured in early winter were at their maximum level in animals from 2 to 10 years of age, declined significantly at 11 years, and remained at a low level until 16 years, the age of the oldest animal so measured. That decline is presumably caused by a lowering in metabolic efficiency related to general senescence, including tooth deterioration.

From conception, males grew more rapidly, in terms of absolute rate, than females. They also continued to grow later in life, to an age of at least 5 years. The presence of spermatozoa in the testes and epididymides suggested that yearling males were physiologically capable of breeding. However under the circumstances which prevailed in the parks males do not usually have the opportunity to breed until at least 4 years of age (Struhsaker, 1967). The size of testes as measured in post-rut condition increased with age until at least 6 years, and remained high until 13 years, the age of the oldest bull examined. The oldest male examined during the rut, aged 12 years, was in breeding condition and possessed a harem. The data suggest that few if any bulls lived to an age of reproductive incapacity. Antlers were produced annually, beginning at 1 year of age. The size of successive sets, on the average, increased to reach a maximum at 6 or 7 years of age. Kidney fat deposits of males as measured in early winter, increased in relation to age to 2 years, remained fairly stable until 7 years, then decreased significantly between 7 and 8 and, until 13 years, the age of the oldest specimen measured, remained at a uniform level lower than in any class except calves. Perhaps the accumulated effects of "wear and tear" on the organism, including tooth deterioration, cause a decline in metabolic efficiency to become evident between 7 and 8 years of age. However, the following items of evidence suggest that

there may be an increase in breeding activity at about that age which could cause older bulls to more completely deplete their energy reserves. The three bulls shot during September (when most breeding occurred) that were with cows, were 7, 8, and 12 years old. There was no decline in the post-rut weight of testes between 6 years of age, when maximum size was first reached, and 13 years, the age of the oldest specimen measured. Similarly, there was no significant decline in antler weight from 7 until 13 years of age.

Inasmuch as males attain greater body size than females, the food requirements for growth and maintenance (Brody, 1945), can be expected to be greater in males. Data are not available to directly compare the nutritional requirements of antler production and breeding activity in males with those of foetal growth and lactation in females. However, the results of the comparisons of rates of tooth wear, if the interpretation is correct, indicate that from the time when complete permanent dentition is obtained at about 2 years of age, females have a lower food intake than males. This suggests that females have a lower food requirement than males, which would confer on them an advantage in survival.

Probably differences between males and females in their seasonal timing of storage and depletion of energy are more important than total food requirements in placing males at a disadvantage in survival. The slow recovery of fat reserves in all wapiti, through the summer from a spring low, coincides with an abundance of food on the one hand, and on the other, muscular and skeletal growth in the younger animals, antler growth in the bulls, and lactation in the cows. In the rut, the deposition of fat is at least slowed in yearling and 2-year-old males, and in adult males high physical activity and partial fasting are accompanied by a heavy and rapid drain on fat reserves. The fat reserves of females remain high through

that period.

A period of negative energy balance in both sexes occurs from about December until April or May. Perhaps, as the experiments of Magruder *et al.* (1957) have shown for white-tailed deer, and Wood *et al.* (1962) have shown for black-tailed and mule deer, wapiti fed *ad libitum* on a high quality diet in winter would exhibit a negative energy balance with a voluntary reduction in food intake. However, in the areas where the present study was conducted, the low temperatures coupled with snow cover and seasonally inferior food supply would probably impose a more stringent limitation on the energy balance than the potential for the species in winter. In any case, males older than calves having entered the winter with lower fat reserves than females, tend to reach potentially critical levels before females. They are thus more vulnerable to death at that time caused basically by an inadequacy of energy.

It was previously mentioned that, perhaps as a result of an increase in breeding activity, males 8 years of age and older entered the winter with lower fat reserves than younger males. It is suggested therefore that the marked increase in non-harvest mortality of males after 7 years of age, as indicated by the composition of the slaughtered samples, was a result of that condition, i.e. that older bulls are particularly prone to death in late winter in which the primary cause is an inadequacy of energy.

Few dead wapiti have been found in any of the parks in recent years when the season and cause of death could be determined. However, R. Jones, Chief Park Warden, and A. Roberts, retired Park Warden, mentioned (pers commun) that in earlier years when Elk Island was heavily stocked, dead or dying wapiti were found commonly in severe winters. They were usually found late in winter, and large bulls and calves predominated. Anderson (1958)

mentioned a higher rate of winter deaths of bulls than cows on the National Elk Refuge in Jackson Hole. Darling (1939:115) writing of red deer stated, "Indeed, the season of April and early May is the time when many deer of both sexes die, but there is an undoubtedly higher mortality among stags than among hinds. It is the common experience to find the population of deer in a given area composed of females to males in the proportion of two to one, though among the calf crop the ratio is almost equal, or if anything in favour of the males."

Several of the parasites found were sufficiently common to suggest a potential for affecting a large proportion of the population: giant liver fluke, fringed tapeworm, hydatid cyst, thread lungworm, biting louse, and winter tick. Their effects while probably slight in most instances, would tend to lower the tolerance of the host to other adverse circumstances. In winter male wapiti have lower fat reserves than females. Those parasites which infected the sexes in equal incidence and equal loads could help to make that sex difference operate to cause a proportionately higher winter-kill in males than in females.

Two of the parasites studied appeared to infect one sex more frequently than the other. The incidence of infections with giant liver fluke was significantly higher in females than in males in Waterton Lakes. Thus, any contribution which it makes to mortality in that park can be expected to affect proportionately more females than males. However, the giant liver fluke was absent or rare in Jasper, and in Banff apparently occurred only in immigrants from Kootenay.

In the research series, males had a significantly higher incidence of infections with winter tick than females. As the weakening effect of that parasite on its host is greatest in late winter and spring, it would

add to the effect of the sex difference in fat reserves, to make males more vulnerable to winter-kill than females. The winter tick has been recorded in all of the parks studied except Waterton Lakes (Cowan, 1951; Love, 1955; Gregson, 1956) and is probably present there as well. If a sex difference in incidence is universal, it may contribute to a sex difference in life expectancy of wapiti in all of those areas.

It was initially hypothesized that the intense social interactions of the rut might stress males more than females to an extent that, through exhaustion of the adrenal cortex, the males would be less able to adapt to the effects of other stressor agents. The data obtained on adrenal weights and zona glomerulosa widths did not reveal any evidence of such a relationship. However, it was shown that those measurements varied considerably among specimens of the same sex and age collected at the same time of year. It was also shown that the adrenal measurements of animals of which the homeostasis had been severely insulted, were not recognizably different from those of untreated specimens. For those reasons the results are not conclusive.

A seasonal trend in width of the zona glomerulosa was noted in wapiti of both sexes, the width being greatest from June until September and least from December to April. It is suggested that the reduction in width was caused by an increase in secretion of ACTH, which in turn was related to the stressful effects of low temperature, accumulation of snow, and the seasonally inferior food supply of winter.

Cowan (1950) suggested that disproportionate sex ratios in various ungulates might be related to overstocking and range depletion. Taber and Dasmann (1954), Robinette *et al.* (1957) and Klein and Olsen (1960) discussed evidence for such a relationship in deer of the genus *Odocoileus*.

Peek *et al.* (1967) attributed a disparity between the sexes in wapiti in the Gallatin drainage in Montana to range depletion.

Adverse nutritional conditions such as would occur with overstocking and range depletion would probably increase the sex difference in mortality in wapiti. In the present study the fat reserves of males in early winter were significantly smaller than those of females, in broad age groups older than calves. We might therefore expect that in each of those age groups males would have a lower tolerance to food shortage. However, in the present study, which was conducted under reasonably favorable circumstances of stocking and forage supply, the mortality of males did not greatly exceed that of females before 1-1/2 years of age. The age at which the mortality rate of males began to appreciably exceed that of females is not known, but there were indications that the difference became marked after 7 years of age. It is evident that beyond whatever age the mortality rate of males begins to exceed that of females, the sex ratio will become more unbalanced with increasing age until in the oldest classes only females remain. The absence of substantial exploitation being a major factor predisposing overstocking in cervids, and reduced reproduction and survival of young of both sexes being characteristic of such a situation, it follows that populations affected by overstocking tend to have a higher proportion of old animals than populations on understocked ranges. Therefore, even if malnutrition were not to increase the sex difference in mortality at any given age (Reasons have been shown to expect that it would.), a population of wapiti suffering the effects of overstocking could be expected to have a greater disparity of the sexes than one on an understocked range, simply as a function of greater age. Conversely, exploitation, by reducing the proportion of old animals, and

increasing the proportion of young would bring the sex ratio nearer to 1:1.

Differences in the age distribution of populations and in the intensity of range use have probably contributed to the variation in sex ratios observed in this and previous studies. However in view of the apparently small difference between non-harvest losses of males and females in Elk Island, and indications of bias favoring observation of females in the mountain parks, the results of classified counts in mountainous areas should be interpreted with caution.

In considering the evolutionary significance of the differences in distribution and mortality between male and female wapiti Rand's (1952) comments are pertinent. He pointed out that in some birds, different distribution of the sexes at times other than the breeding season helps limit intra-specific competition for food. Similarly in wapiti, many males apparently disperse from the ranges where they were reared to vacant or less densely inhabited areas, often to winter ranges with deeper snow. The tendency for an earlier death in males, by leaving fewer of them in the population, would be expected to contribute to the same effect which is to leave more food and space for females and young, and thus contribute to sustaining a high reproductive success.

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Appendix 1. Approximate mean* annual total precipitation and mean* daily temperature for January, April, July, and October for parks studied

Park	Precipitation (inches)	Mean daily temperature (°F)			
		Jan	April	July	Oct
Elk Island	16-18	5-10	35-40	60-65	40-45
Jasper	18-20	10-15	35-40	55-60	40-45
Banff	20-22	10-15	35-40	55-60	35-40
Kootenay	20-22	10-15	35-40	60-65	35-40
Waterton Lakes	22±	15-20	35-40	55-60	40-45

* Mean of 1921-1950 incl. from Atlas of Canada (Dept. Mines and Tech. Surveys, 1957)

Appendix 2. Cervid population estimates* and numbers slaughtered, Elk Island, 1959-1966.

Date	Wapiti		Moose		Mule deer and white-tailed deer		Source of data
	Pop.†	Slaughtered	Pop.	Slaughtered	Pop.	Slaughtered	
Oct, '59	640		120		10		Computed
Dec, '59		410		141		0	
Feb, '60	230		80		10		Flock (1960)
Nov, '60	270		120		70		Computed
Dec, '60		106		24		0	
Feb, '61	160		100		70		Lovaas (1961)
Dec, '61	230		150		100		Blood (1962)
Nov, '63	330		260		70		Computed
Dec, '63		87		87		0	
Jan, '64	240		170		70		Blood (1964)
Jan, '66	280		330		40		Blood (1966)

* Computed population estimates determined by adding following slaughter and post-slaughter count.

† Population estimates rounded to nearest 10.

Appendix 3. Park Wardens' counts of wapiti in Jasper, 1959 to 1966

Year	Drainage, and number of wapiti		
	Athabasca	Brazeau	Total
1959 (Nov)	1040	?	?
1960 (Dec)	770	130	900
1965 (Oct-Nov)	1600	190	1790
1966 (Oct-Nov)	1630	100	1730

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Appendix 4. Park wardens' counts* of wapiti in Banff, 1962 to 1966

Year	Valleys, and numbers of wapiti			Total
	Bow	Cascade Panther and Red Deer	Other valleys	
1962	410	940	250	1600
1963	610	1120	400	2130
1964	360	1010	240	1610
1965	250	1000	190	1440
1966	260	590	280	1130

* Counts conducted in one-week period in late September and early October.

Summary of the results of the analysis of variance				
Source of variation				
Degrees of freedom				
Mean square				
F value				
Probability				
Between groups	1	10.00	10.00	0.01
Within groups	10	1.00	1.00	0.10
Total	11	11.00	11.00	0.11

Appendix 5. Park wardens' late-winter counts of wapiti in Waterton Lakes, 1953 to 1967

Year	No. of wapiti
1953-54	830
1954-55	1030
1955-56	1200
1956-57	1000
1960-61	650
1961-62	930
1964-65	680
1965-66	550
1966-67	690

Appendix 6. Complete information on male wapiti in research series except for data on ectoparasites

Age (yr)	Date	Spec. No.	Drainage	Hind foot length (cm)	Chest girth (cm)	Body wt. (kg)	Kidney fat wt. (g)	Kidney fat index (%)	Dry antler wt. (g)	Antler condition	Wt. of testes (g)	Abundance of spermatozoa Epididymides	Width of zona glomerulosa (mm)	Adrenal wt. (g)	<i>Fascioloides magna</i>	Hydatid cysts	<i>Thysanotoma actinoides</i>	<i>Dietyocaulus viviparus</i>
1	Aug 2, '61	6	Cascade	61.6	121.3	-	140	28	-	vascular	70	0	0.48	5.31	0	0	13	infection
1	Aug 4, '61	7	Cascade	61.6	124.5	-	60	10	-	vascular	86	0	.56	6.44	0	0	54	infection
1	Sept 14, '61	14	Cascade	63.5	128.3	-	185	47	-	vascular	75	3	.67	5.65	0	0	28	0
1	Sept 14, '62	97	Cascade	64.8	133.4	187	152	32	136	vascular	42	1	.46	5.57	0	0	41	0
1	Oct 14, '62	100	Cascade	67.3	146.0	227	246	66	454	hardened	101	1	.41	6.92	0	0	3	0
1	Oct 15, '61	23	Bow	65.4	131.4	206	380	106	-	hardened	68	1	.49	5.37	0	0	0	0
1	Oct 15, '61	24	Bow	64.1	141.0	244	552	135	272	hardened	103	2	.40	6.48	0	0	0	0
1	Oct 17, '61	25	Cascade	63.5	142.2	201	290	86	544	hardened	72	2	.61	6.06	0	0	3	0
1	Nov 29, '61	34	Bow	66.0	139.7	225	214	55	363	hardened	50	0	.50	9.06	0	0	-	0
1	Dec 4, '61	39	Bow	61.0	127.0	-	106	34	204	hardened	48	0	.43	5.77	0	0	-	0
1	Dec 15, '61	43 ^b	Bow	66.7	134.6	214	-	-	408	hardened	-	0	-	-	0	0	4	0
1	Dec 15, '61	45 ^a	Bow	63.5	132.1	199	326	84	-	hardened	-	0	.43	-	0	0	2	0
1	Dec 18, '61	50	Bow	64.8	134.6	198	210	68	318	hardened	78	0	.57	6.64	0	0	6	0
1	Jan 11, '62	60	Bow	63.5	139.7	198	306	82	249	hardened	42	0	.49	7.31	0	0	-	0
1	Jan 16, '62	65	Bow	64.1	144.8	180	132	41	227	hardened	51	0	.44	-	0	0	-	0
1	Feb 19, '62	71	Kootenay	66.7	132.7	175	51	15	181	hardened	33	0	.71	8.67	scars	0	1	0
1	Mar 28, '62	74	Red Deer	66.0	132.1	174	36	13	181	hardened	-	0	.44	5.45	0	0	0	0
1	Mar 30, '62	77	Red Deer	62.9	141.0	157	38	12	454	hardened	55	0	.48	5.51	0	0	0	0
1	May 28, '62	82	Red Deer	65.4	135.9	196	49	12	227	hardened	60	0	.44	5.11	0	0	1	infection
2	June 2, '62	87	Cascade	62.9	123.2	138	33	8	23	vascular	34	0	0.65	6.83	0	0	6	infection
2	June 2, '62	88	Cascade	62.9	131.4	165	20	5	43	vascular	40	0	.69	7.19	0	0	0	infection
2	July 23, '62	92	Red Deer	65.4	141.0	207	102	15	635	vascular	118	0	.44	8.62	infection	0	4	infection
2	July 27, '61	3	Cascade	65.4	139.7	-	125	23	-	vascular	79	0	.57	6.12	0	infection	1	0
2	Sept 11, '62	93	Red Deer	67.9	162.6	-	536	97	1950	hardened	164	2	.67	8.92	0	0	0	0
2	Sept 12, '62	95	Cascade	68.6	156.2	-	398	64	907	hardened	130	2	.52	8.27	0	0	0	0
2	Oct 15, '62	104	Cascade	66.0	153.7	-	450	125	1451	hardened	114	2	.43	-	0	0	3	0
2	Nov 7, '61	27	Red Deer	67.3	148.6	303	-	-	1225	hardened	68	1	.60	-	0	0	-	0
2	Nov 8, '61	28	Cascade	66.0	143.5	301	402	80	1089	hardened	86	-	.60	-	0	0	-	0
2	Nov 30, '61	37	Bow	64.1	156.2	274	454	85	1905	hardened	81	0	.39	7.20	0	0	-	0
2	Dec 11, '61	42	Bow	67.3	149.9	277	353	55	1383	hardened	64	1	.52	7.75	0	0	-	0
2	Dec 19, '61	54	Bow	67.3	154.9	284	458	86	2222	hardened	68	0	.41	7.36	infection	0	-	0
2	Jan 8, '62	56	Bow	66.0	146.0	238	285	55	1430	hardened	64	1	.34	7.64	0	0	-	0
2	Jan 11, '62	61	Bow	63.5	144.8	228	310	74	1678	hardened	58	0	.37	8.27	0	0	-	0
2	Feb 6, '63	105	Red Deer	-	-	-	104	30	1444	hardened	-	-	-	8.30	0	0	0	0
2	Feb 19, '62	70	Kootenay	68.6	151.8	-	71	16	1542	hardened	69	0	.52	7.42	infection	infection	0	0
2	Apr 2, '62	79	Kootenay	66.0	136.5	187	28	9	1451	hardened	54	0	.46	7.88	infection	0	0	0
6	June 1, '62	86	Cascade	67.9	151.8	272	50	7	1.4	vascular	58	0	0.84	10.00	0	0	0	0
3	July 14, '61	2	Red Deer	67.9	149.9	-	166	22	-	vascular	149	0	.59	8.67	0	0	2	infection
10	Aug 19, '65	106	Red Deer	69.8	202.6	449	1110	100	7.5	hardened	327	3	-	13.73	0	0	0	0
7	Sept 8, '65	107	Red Deer	66.0	177.8	384	740	94	10.3	hardened	455	2	-	14.09	0	0	0	0
5	Sept 11, '61	11	Cascade	69.2	156.2	381	431	55	6.1	hardened	274	3	.55	10.86	0	0	0	0
9	Sept 12, '61	12	Cascade	63.5	160.0	323	579	89	10.3	hardened	143	3	.79	13.17	0	0	0	0
10	Sept 15, '61	17	Cascade	71.1	188.0	-	570	51	12.2	hardened	328	1	.50	14.02	0	0	0	0
12	Sept 27, '65	108	Cascade	68.6	186.7	-	308	30	11.3	hardened	357	3	-	-	0	0	0	0
5	Oct 11, '61	18	Cascade	66.7	174.0	-	387	75	-	hardened	180	3	.52	-	0	0	0	0
5	Oct 12, '61	21	Cascade	66.0	163.2	-	62	12	5.4	hardened	152	3	.71	8.77	0	0	0	0
5	Oct 13, '62	99	Cascade	67.9	174.0	-	499	88	4.5	hardened	156	3	.59	8.41	0	0	0	0

Appendix 6 Continued

Age (yr)	Date	Spec. No.	Drainage	Hind foot length (cm)	Chest girth (cm)	Body wt. (kg)	Kidney fat wt. (g)	Kidney fat index (%)	Dry antler wt. (g)	Antler condition	Wt. of testes (g)	Abundance of Testes	Epithidymides	Width of zona glomerulosa (mm)	Adrenal wt. (g)	<i>Fascioloides</i> <i>magna</i>	Hydatid cysts	<i>Thysanotoma</i> <i>actinoides</i>	<i>Dictyocaulus</i> <i>viviparus</i>
3	Oct 14, '62	101	Cascade	70.5	167.6	-	482	89	2.6	hardened	156	3	4	.68	9.50	0	0	0	0
12	Oct 19, '65	110	Cascade	68.6	175.3	377	55	7	8.2	hardened	250	2	4	-	-	0	0	0	0
7	Nov 19, '65	113	Bow	70.5	185.4	470	538	64	11.2	hardened	206	3	4	-	10.71	0	0	-	0
8	Nov 29, '61	35	Bow	61.3	162.6	336	133	17	7.6	hardened	120	1	4	.55	11.46	0	0	-	0
8	Nov 30, '61	36	Bow	68.6	167.0	367	212	24	6.6	hardened	128	0	4	.64	10.93	0	infection	-	0
3	Dec 15, '61	44	Bow	68.6	152.4	274	288	60	2.4	hardened	82	0	4	.45	8.89	0	0	0	0
5	Dec 15, '61	48b	Bow	66.0	158.8	291	162	31	4.0	hardened	94	0	4	-	10.10	0	0	-	0
8	Dec 18, '61	51	Bow	67.3	157.5	309	321	42	5.8	hardened	101	1	4	.48	13.79	0	0	0	0
5	Jan 10, '62	59	Cascade	69.8	165.1	320	198	29	5.2	hardened	102	0	4	.59	11.94	0	0	-	0
5	Jan 16, '62	64	Bow	67.3	157.5	306	182	31	5.2	hardened	91	0	4	.38	9.99	0	0	-	0
13	Feb 19, '62	69	Kootenay	64.1	162.6	273	50	7	5.6	hardened	101	1	4	.61	11.21	infection	0	0	0
6	May 29, '62	84	Red Deer	64.1	147.3	236	54	10	0.6	vascular	47	0	0	.58	8.88	0	0	0	0

Appendix 7. Complete information on female wapiti in research series except for data on ectoparasites

Age (yr)	Date	Spec no.	Drainage	Hind foot length (cm)	Chest girth (cm)	Body wt (kg)	Kidney fat wt (g)	Kidney index	Udder fat (%)	Udder	Uterus	Width of zona glomerulosa (mm)	Adrenal wt (g)	<i>Fascioloides magna</i>	Hydatid cysts	<i>Thysanosoma actinoides</i>	<i>Dictyocaulus viviparus</i>
<1	Feb 16, '62	68	Red Deer	56.5	-	-	20	10		dry	quiescent	-	-	0	0	0	0
<1	Oct 21, '65	111	Bow	59.1	119.4	129	379	147		dry	quiescent	-	3.65	0	0	0	0
1	Aug 4, '61	8	Cascade	60.3	121.3	-	110	23		dry	quiescent	0.65	6.13	0	0	6	infection
1	Aug 5, '61	9	Cascade	61.0	121.9	163	162	36		dry	quiescent	.70	5.90	0	0	23	0
1	Sept 12, '62	94	Cascade	60.3	139.7	-	310	81		dry	quiescent	.50	5.19	0	0	24	infection
1	Sept 13, '62	96	Cascade	63.5	132.1	186	693	186		dry	quiescent	.85	7.29	0	0	13	0
1	Oct 12, '61	19	Red Deer	62.9	128.3	-	220	63		dry	?	.59	6.03	0	0	0	0
1	Oct 12, '61	22	Red Deer	60.3	132.1	-	304	85		dry	quiescent	.61	-	0	0	0	infection
1	Nov 27, '61	32	Bow	62.2	141.6	183	287	92		dry	quiescent	.51	-	0	0	1	0
1	Dec 4, '61	40	Bow	61.0	136.5	185	360	112		dry	quiescent	.58	6.68	0	0	-	0
1	Dec 11, '61	41	Bow	62.2	130.8	203	557	153		dry	quiescent	.39	6.85	0	0	-	0
1	Dec 15, '61	46	Bow	62.2	127.0	181	792	248		dry	quiescent	.42	6.87	0	0	0	0
1	Jan 8, '62	55	Bow	62.2	132.1	179	290	74		dry	quiescent	-	-	0	0	0	0
1	Jan 11, '62	63	Bow	61.0	129.5	169	264	78		dry	quiescent	.27	5.18	0	0	-	0
1	Apr 4, '62	80	Bow	64.8	129.5	149	45	18		dry	quiescent	.39	6.05	infection	0	0	0
1	May 31, '62	85	Red Deer	64.8	129.5	172	34	8		dry	quiescent	.47	6.49	0	0	0	infection
2	June 4, '62	89	Cascade	62.9	124.5	150	54	13		dry	quiescent	.72	6.23	0	0	1	0
2	July 27, '61	4	Cascade	62.2	134.6	-	159	39		dry	quiescent	.68	8.78	0	0	5	infection
2	July 31, '61	5	Cascade	61.6	125.7	-	184	41		dry	quiescent	.53	6.04	0	0	4	infection
2	Sept 20, '62	98	Red Deer	64.4	149.2	217	690	147		dry	?	.46	8.71	0	0	0	0
2	Nov 27, '61	30	Bow	63.5	149.9	222	502	129		dry	pregnant	.52	6.50	0	0	-	0
2	Nov 28, '61	33	Bow	61.0	139.7	220	470	126		dry	pregnant	.48	6.95	0	0	-	0
2	Dec 15, '61	43a	Bow	64.8	146.0	254	538	137		dry	pregnant	.44	-	0	0	0	0
2	Dec 15, '61	47	Bow	62.9	138.4	237	796	206		dry	pregnant	.38	8.47	infection	0	0	0
2	Jan 11, '62	62	Bow	62.2	142.2	220	421	101		dry	pregnant	.48	6.65	0	0	-	0
2	Jan 16, '62	66	Bow	61.0	138.4	204	453	126		dry	pregnant	.49	7.77	0	0	-	0
2	Feb 15, '62	67	Red Deer	64.8	153.7	237	282	90		dry	pregnant	.45	7.67	0	0	0	0
2	Feb 20, '62	72	Kootenay	61.0	140.3	178	250	69		dry	pregnant	.45	-	infection	0	0	1
6	June 12, '62	90	Cascade	62.9	142.2	223	104	17		lact	dilated	.60	-	0	0	0	0
10	June 12, '62	91	Cascade	63.5	141.0	210	39	7		lact	dilated	.65	11.27	0	0	0	0
11	July 9, '61	1	Cascade	63.5	137.2	182	120	20		lact	quiescent	.76	10.42	0	0	0	0
>3	Aug 24, '61	10	Red Deer	64.8	135.2	-	-	-		lact	quiescent	.61	10.80	0	0	0	infection
5	Sept 13, '61	13	Cascade	61.6	158.8	-	766	157		dry	?	.44	8.13	-	-	0	0
4	Sept 15, '61	15	Cascade	61.6	144.8	-	866	188		dry	thickened	.49	6.83	0	0	0	0
3	Sept 15, '61	16	Cascade	64.8	146.1	-	658	122		dry	thickened	.41	7.43	0	0	0	infection
4	Sept 29, '65	109	Cascade	65.4	157.5	283	1411	244		dry	?	-	8.87	0	0	0	0
4	Oct 12, '61	20	Red Deer	63.5	160.1	-	558	118		dry	thickened	.52	-	0	0	0	0
21	Oct 14, '62	102	Cascade	63.5	144.8	238	503	108		dry	quiescent	.64	12.89	0	0	0	0
18	Oct 14, '62	103	Cascade	66.0	141.0	212	106	21		dry	quiescent	.54	11.09	0	infection	0	0
8	Oct 18, '62	26	Cascade	64.8	148.6	-	356	87		lact	thickened	.54	9.55	0	0	0	0
8	Nov 18, '65	112	Red Deer	66.0	157.5	287	1273	232		dry	pregnant	-	7.87	0	0	2	0
8	Nov 27, '61	29	Bow	63.5	147.3	265	654	133		dry	pregnant	.49	10.77	0	-	-	0
3	Nov 27, '61	31	Bow	63.5	147.3	224	525	119		dry	pregnant	.57	8.38	0	0	0	0
>3	Dec 15, '61	45b	Bow	63.5	142.2	254	759	179		dry	pregnant	-	-	0	0	0	0
6	Dec 18, '61	48a	Bow	63.5	146.1	278	852	168		dry	pregnant	.36	8.36	0	0	0	0

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Appendix 7. Continued

Age (yr)	Date	Spec no.	Drainage	Hind foot length (cm)	Chest girth (cm)	Body wt. (kg)	Kidney fat wt (g)	Kidney fat index (%)	Udder	Uterus	Width of zona glomerulosa (mm)	Adrenal wt (g)	<i>Fascioloides magna</i>	Hydatid cysts	<i>Thysanosoma actinoides</i>	<i>Dictyocaulus viviparus</i>
6	Dec 18, '61	49	Bow	64.8	144.8	300	758	141	dry	pregnant	0.52	10.82	0	0	-	0
4	Jan 8, '62	57	Bow	63.5	149.9	259	602	110	dry	pregnant	.45	8.78	0	infection	-	0
9	Jan 8, '62	58	Bow	63.5	153.7	294	508	104	lact	pregnant	.40	9.38	0	0	-	0
10	Feb 21, '62	73	Kootenay	62.2	146.8	221	388	111	dry	pregnant	.56	9.52	dead flukes	0	0	0
6	Mar 29, '62	75	Red Deer	63.5	154.9	237	216	60	dry	pregnant	.47	7.84	0	0	0	0
9	Mar 30, '62	76	Red Deer	65.4	150.5	237	174	31	dry	pregnant	.30	9.80	0	0	0	0
7	Mar 31, '62	78	Red Deer	62.9	152.4	237	176	44	dry	pregnant	.50	7.94	0	0	0	0
4	May 26, '62	81	Cascade	63.5	144.2	220	50	12	lact	dilated	.37	8.71	0	0	0	0
18	May 28, '62	83	Red Deer	67.3	134.6	161	22	4	lact	dilated	.76	11.50	0	0	0	0

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Appendix 8. Ticks (*Dermacentor albipictus*) and lice (*Damalinia concavifrons*) counted on samples of skin from wapiti in research series collected in Banff and Kootenay National Parks and the Ya Ha Tinda Ranch

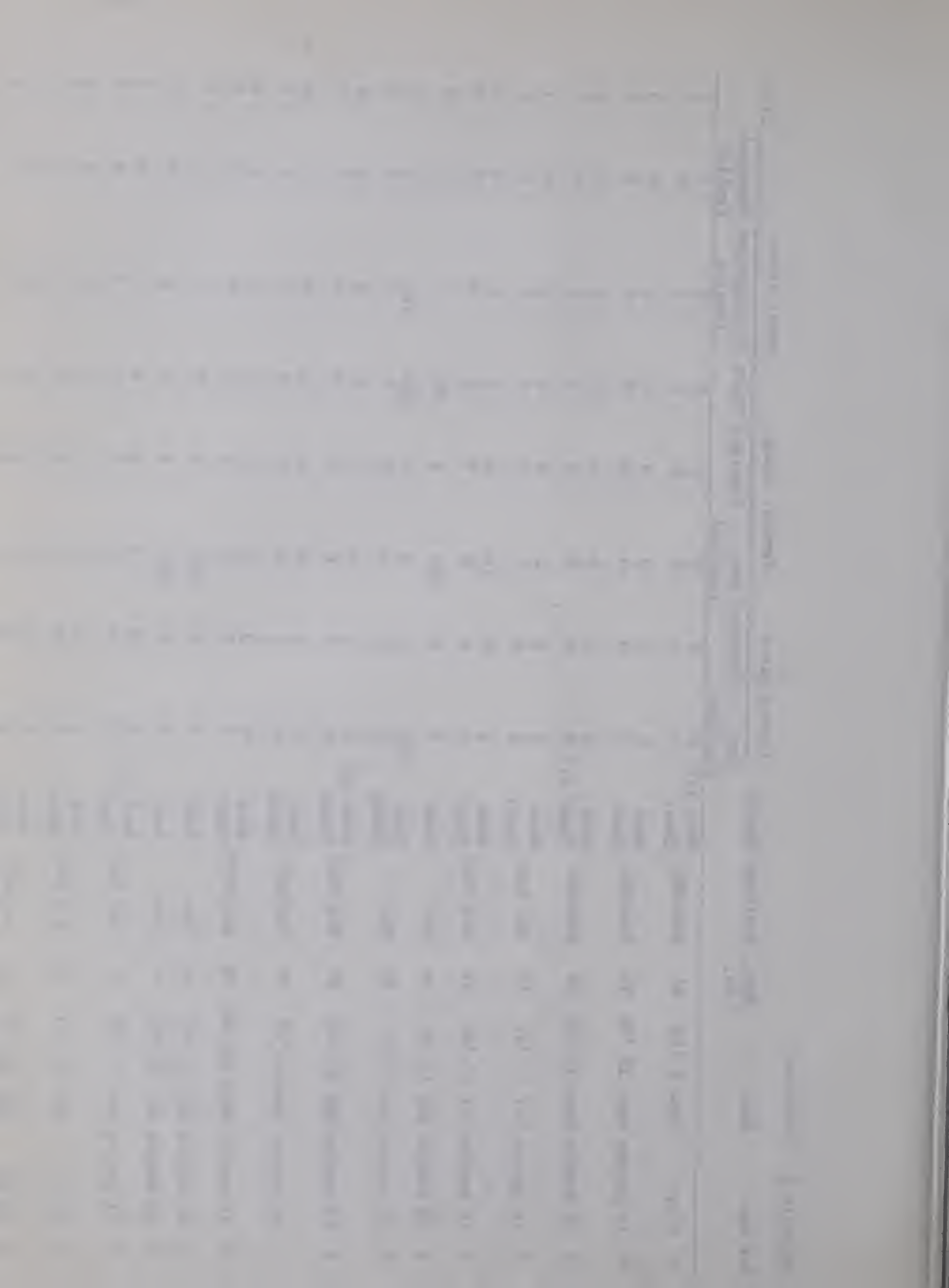
Sex	Age	Date	Spec. No.	Drainage	Sample	Larval ticks		Nymphal ticks		Adult ticks				
						Non-engorged	Engorged	Non-engorged	Engorged	Males	Non-engorged females	Engorged females	Lice	
♂	15 months	Sept 14, '62	97	Cascade	Neck Chest	0	0	0	0	0	0	0	0	0
♂	16 months	Oct 15, '61	23	Bow	Neck Chest	0	0	0	0	0	0	0	0	0
♂	16 months	Oct 15, '61	24	Bow	Neck Chest	30	27	55	0	0	0	0	0	0
♂	16 months	Oct 15, '61	24	Bow	Neck Chest	3	5	5	0	0	0	0	0	0
♂	16 months	Oct 15, '61	24	Bow	Neck Chest	0	0	0	0	0	0	0	0	0
♂	16 months	Oct 17, '61	25	Cascade	Neck Chest	5	0	5	0	0	0	0	0	1
♂	16 months	Oct 17, '61	25	Cascade	Neck Chest	0	0	12	0	0	0	0	0	0
♂	18 months	Dec 15, '61	43b	Bow	Neck	0	0	911	3	4	1	0	0	0
♂	18 months	Dec 15, '61	45	Bow	Neck	0	0	626	41	33	18	0	0	0
♂	18 months	Dec 18, '61	50	Bow	Neck	0	0	1379	28	15	6	0	0	0
♂	20 months	Feb. 19, '62	71	Kootenay	Neck Chest	0	0	61	21	32	11	0	0	0
♂	20 months	Feb. 19, '62	71	Kootenay	Neck Chest	0	0	19	2	0	1	0	0	0
♂	21 months	Mar 28, '62	74	Red Deer	Neck Chest	0	0	52	64	380	227	2	0	0
♂	21 months	Mar 28, '62	74	Red Deer	Neck Chest	0	0	5	6	6	5	0	0	0
♂	21 months	Mar 30, '62	77	Red Deer	Neck Chest	0	0	16	9	132	101	0	0	0
♂	21 months	Mar 30, '62	77	Red Deer	Neck Chest	0	0	0	0	4	1	0	0	0
♂	23 months	May 28, '62	82	Red Deer	Neck Chest	0	0	0	0	2	2	0	9	6
♂	23 months	May 28, '62	82	Red Deer	Neck Chest	0	0	0	0	0	0	0	0	0
♂	24 months	June 2, '62	87	Cascade	Neck Chest	0	0	0	0	1	0	0	0	0
♂	24 months	June 2, '62	87	Cascade	Neck Chest	0	0	2	0	0	0	0	17	14
♂	24 months	June 2, '62	88	Cascade	Neck Chest	0	0	0	0	0	0	0	0	0
♂	24 months	June 2, '62	88	Cascade	Neck Chest	0	0	2	0	0	0	0	0	14
♂	25 months	July 23, '62	92	Red Deer	Neck Chest	0	0	0	0	0	0	0	0	0
♂	25 months	July 23, '62	92	Red Deer	Neck Chest	0	0	0	0	0	0	0	0	0

Appendix 8. Continued

Sex	Age	Date	Spec. No.	Drainage	Sample	Larval ticks		Nymphal ticks		Adult ticks		Lice
						Non-engorged	Engorged	Non-engorged	Engorged	Males	Non-engorged females	
♂	27 months	Sept 11, '62	93	Red Deer	Neck 1/2 Chest	0	0	0	0	0	0	0
						0	0	0	0	0	0	0
♂	27 months	Sept 12, '62	95	Cascade	Neck 1/2 Chest	0	0	0	0	0	0	0
						0	0	0	0	0	0	0
♂	28 months	Oct 15, '62	104	Cascade	Neck Chest	0	0	0	0	0	0	0
						0	0	0	0	0	0	0
♂	30 months	Dec 19, '61	54	Bow	Neck	0	0	56	0	0	0	0
♂	32 months	Feb 19, '62	70	Kootenay	Neck Chest	0	0	131	149	37	1	0
						0	0	5	1	0	0	0
♂	34 months	Apr 2, '62	79	Kootenay	Neck Chest	0	0	0	220	68	3	0
						0	0	20	7	9	0	0
♂	5 yr	Oct 11, '61	18	Cascade	Neck Chest	0	0	0	1	0	0	0
						0	0	0	0	0	0	0
♂	5 yr	Oct 12, '61	21	Cascade	Neck 1/2 Chest	0	0	0	0	0	0	0
						0	0	0	0	0	0	0
♂	5 yr	Oct 13, '62	99	Cascade	Neck Chest	1	0	0	0	0	0	0
						4	0	0	0	0	0	0
♂	3 yr	Oct 14, '62	101	Cascade	Neck Chest	1	0	28	0	0	0	0
						0	0	10	0	0	0	0
♂	3 yr	Dec 15, '61	44	Bow	Neck	0	0	1035	7	5	0	0
♂	5 yr	Dec 15, '61	48b	Bow	Neck	0	0	210	31	7	0	0
♂	8 yr	Dec 18, '61	51	Bow	Neck	0	0	38	1	0	0	0
♂	13 yr	Feb 19, '62	69	Kootenay	Neck Chest	0	0	123	181	41	3	7
						0	0	30	22	2	0	0
♂	6 yr	May 29, '62	84	Red Deer	Neck 1/2 Chest	0	0	0	2	0	0	0
						0	0	0	0	0	0	0

Appendix 8. *Continued*

Sex	Age	Date	Spec. No.	Drainage	Sample	Larval ticks		Nymphal ticks		Adult ticks		Lice
						Non-engorged	Engorged	Non-engorged	Engorged	Non-engorged	Engorged	
						engorged	engorged	engorged	engorged	females	females	
♂	6 yr	June 1, '62	86	Cascade	Neck 1/2 Chest	0	0	0	0	0	0	0
♀	15 months	Sept 12, '62	94	Cascade	Neck Chest	0	0	0	0	0	0	0
♀	15 months	Sept 13, '62	96	Cascade	Neck Chest 1/2	0	0	0	0	0	0	0
♀	16 months	Oct 12, '62	19	Red Deer	Neck Chest	2	0	4	0	0	0	1
♀	16 months	Oct 12, '62	22	Red Deer	Neck Chest	1	0	10	0	0	0	0
♀	18 months	Dec 15, '61	46	Bow	Neck	0	0	593	9	20	4	0
♀	22 months	Apr 4, '62	80	Bow	Neck Chest	200	0	0	6	218	124	0
♀	23 months	May 31, '62	85	Red Deer	Neck 1/2 Chest	0	0	0	0	0	2	0
♀	24 months	June 4, '62	89	Cascade	Neck Chest	0	0	0	0	0	0	12
♀	27 months	Sept 20, '62	98	Red Deer	Neck Chest	0	0	0	0	0	0	0
♀	30 months	Dec 15, '62	43	Bow	Neck	0	0	453	2	0	1	0
♀	30 months	Dec 15, '62	47	Bow	Neck	0	0	1341	4	1	0	0
♀	32 months	Feb 15, '62	67	Red Deer	Neck 1/2 Chest	0	0	0	0	0	0	0
♀	4 yr	Oct 12, '61	20	Red Deer	Neck Chest	0	0	0	0	0	0	0
♀	21 yr	Oct 14, '62	102	Cascade	Neck Chest	0	0	0	0	0	0	0



Appendix 9. Average numbers of ticks (*Dermacentor albipictus*) of each life stage on skin samples* of wapiti collected in Banff and Kootenay National Parks, and the Ya Ha Tinda Ranch, 1961 and 1962

Period of collection	Stage of tick	Age and sex of wapiti					
		15-25 months		27-37 months		>39 months	
		♂	♀	♂	♀	♂	♀
September	Larva	0	0	0	0	-	-
	Nymph	0	0	0	0	-	-
	Adult	0	0	0	0	-	-
October	Larva	23	2	0	(1)	2	0
	Nymph	41	7	0	-	10	2
	Adult	0	0	0	-	0	0
December	Larva	0	0	0	(0)	0	(4)
	Nymph	996	602	56	900	441	-
	Adult	26	0	0	0	11	-
February	Larva	0	-	0	0	0	0
	Nymph	103	-	211	0	356	298
	Adult	44	-	188	0	207	253
March, April	Larva	0	200	0	0	-	0
	Nymph	76	51	23	-	-	6
	Adult	429	348	307	-	-	86
May, June	Larva	0	0	-	-	0	0
	Nymph	1	0	-	-	2	1
	Adult	2	0	-	-	0	2
July	Larva	0	-	-	-	-	-
	Nymph	0	-	-	-	-	-
	Adult	0	-	-	-	-	-
		(1)	(0)	(0)	(0)	(0)	(0)

* December samples consisted of collar, 25 cm wide immediately posterior to ears. Other samples included collar plus rectangles 25 cm by 12.5 cm from each side of chest. Numbers of wapiti sampled, in parentheses.

Appendix 10. Incidence* of ticks (*Dermacentor albipictus*) on skin samples† from wapiti collected at different times of the year in Banff and Kootenay National Parks and the Ya Ha Tinda Ranch, 1961 and 1962

Period collected	Age and sex of wapiti					
	15-25 months		27-37 months		>39 months	
	♂	♀	♂	♀	♂	♀
September	0/1	0/2	0/2	0/1	0/0	0/0
October	3/3	2/2	0/1	0/0	3/4	1/4
December	3/3	1/1	1/1	2/2	3/3	0/0
February	1/1	0/0	1/1	0/1	1/1	1/1
March and April	2/2	1/1	1/1	0/0	0/0	2/2
May and June	3/3	0/2	0/0	0/0	1/2	1/3
July	0/1	0/0	0/0	0/0	0/0	0/1
October through June	12/12	4/6	3/4	2/3	8/10	5/10

* Number of specimens on which ticks were found/number of specimens sampled.

† December samples consisted of collar, 25 cm wide immediately posterior to ears. Other samples included collar plus rectangle ten inches by 12.5 cm, taken from each side of chest.

1000

1000

Date	Time	Lat	Long	Alt	Wind	Sea	Weather	Remarks
10/10/19	0800	10 10	10 10	10	10	10	10	10
10/10/19	0900	10 10	10 10	10	10	10	10	10
10/10/19	1000	10 10	10 10	10	10	10	10	10
10/10/19	1100	10 10	10 10	10	10	10	10	10
10/10/19	1200	10 10	10 10	10	10	10	10	10
10/10/19	1300	10 10	10 10	10	10	10	10	10
10/10/19	1400	10 10	10 10	10	10	10	10	10
10/10/19	1500	10 10	10 10	10	10	10	10	10
10/10/19	1600	10 10	10 10	10	10	10	10	10
10/10/19	1700	10 10	10 10	10	10	10	10	10
10/10/19	1800	10 10	10 10	10	10	10	10	10
10/10/19	1900	10 10	10 10	10	10	10	10	10
10/10/19	2000	10 10	10 10	10	10	10	10	10
10/10/19	2100	10 10	10 10	10	10	10	10	10
10/10/19	2200	10 10	10 10	10	10	10	10	10
10/10/19	2300	10 10	10 10	10	10	10	10	10
10/10/19	2400	10 10	10 10	10	10	10	10	10

1000

Appendix 11. Numbers of wapiti removed from Elk Island,
March 1947 to January 1958, separated as to
sex and method of removal

Sex	Method of removal	Year of removal*										Total
		1948 -49	1949 -50	1950 -51	1951 -52	1952 -53	1953 -54	1954 -55	1955 -56	1956 -57	1957 -58	
Male	Slaughter	155	12	1	37	36	-	127	76	130	143	717
	Capture	14	22	3	5	-	18	-	26	-	-	88
	Total	169	34	4	42	36	18	127	102	130	143	805
Female	Slaughter	97	1	2	6	75	-	74	-	168	141	564
	Capture	43	26	28	15	-	101	-	84	-	-	297
	Total	140	27	30	21	75	101	74	84	168	141	861
Not speci- fied	Slaughter	-	-	-	-	-	-	4	-	6	3	13
	Capture	-	-	-	-	-	-	-	-	3	-	3
	Total	-	-	-	-	-	-	4	-	9	3	16
Both sexes	Total	309	61	34	63	111	119	205	186	307	287	1682

* Year measured from June 1 to May 31.

TABLE 1. Data on the number of fish caught in the trap during the first 10 days of the experiment. The number of fish caught in the trap during the first 10 days of the experiment is given in the first column. The number of fish caught in the trap during the first 10 days of the experiment is given in the first column. The number of fish caught in the trap during the first 10 days of the experiment is given in the first column.

Experiment 1: Day 1											
Day	1	2	3	4	5	6	7	8	9	10	Total
1	10	15	20	25	30	35	40	45	50	55	385
2	12	18	22	28	32	38	42	48	52	58	410
3	14	20	24	30	34	40	44	50	54	60	438
4	16	22	26	32	36	42	46	52	56	62	464
5	18	24	28	34	38	44	48	54	58	64	492
6	20	26	30	36	40	46	50	56	60	66	518
7	22	28	32	38	42	48	52	58	62	68	544
8	24	30	34	40	44	50	54	60	64	70	570
9	26	32	36	42	46	52	56	62	66	72	596
10	28	34	38	44	48	54	58	64	68	74	622
Total	100	120	140	160	180	200	220	240	260	280	1900

1. The number of fish caught in the trap during the first 10 days of the experiment is given in the first column.

Appendix 12. Numbers of wapiti removed* from Jasper prior to February, 1957

Period	Number	Period	Number
1942-43	127	1948-49	103
1944-45	250	1952-53	78
1945-46	197	1953-54	60
1946-47	375	1954-55	137
1947-48	219	1956-57	152

* Shot in winter.

TABLE 1
 SUMMARY OF THE DATA FOR THE FIRST 100 OBSERVATIONS

Year	Month	Day	Time
1950	January	1	12:00
1950	January	2	12:00
1950	January	3	12:00
1950	January	4	12:00
1950	January	5	12:00
1950	January	6	12:00
1950	January	7	12:00
1950	January	8	12:00
1950	January	9	12:00
1950	January	10	12:00

(Continued on next page)

Appendix 13. Numbers of wapiti of each age group and sex removed* from Banff prior to February 1957

Year	Valleys hunted	<1 yr		≥1 yr		Total
		♂	♀	♂	♀	
1944-45	Bow	4	20	41	135	200
1945-46	"	30	25	80	217	352
1946-47	"	36	23	74	176	309
1947-48	"	22	18	33	181	254
1948-49	Bow and Cascade	5	12	8	78	103
1949-50	" " "	16	22	41	191	270
1950-51	" " "	10	6	46	81	143
1951-52	" " "	8	5	20	69	102
1953-54	Bow	5	2	13	33	53
1954-55	"	-	-	-	7	7
1955-56	"	-	-	5	5	10
Total		136	133	361	1173	1803

* Shot in winter. In all years except 1954-55 and 1955-56 animals were shot without deliberate selection.

(1) The first group of cases is that in which the defendant is a minor, and the victim is an adult. In such cases, the defendant is usually charged with a crime of sexual nature, and the victim is usually charged with a crime of sexual nature.

Case No.	Defendant		Victim		Charge	Disposition
	Name	Age	Name	Age		
101	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
102	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
103	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
104	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
105	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
106	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
107	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
108	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
109	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
110	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
111	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
112	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
113	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
114	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
115	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
116	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
117	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
118	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
119	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10
120	John Doe	18	Jane Smith	25	Sexual Assault	10-10-10

(2) The second group of cases is that in which the defendant is an adult, and the victim is a minor. In such cases, the defendant is usually charged with a crime of sexual nature, and the victim is usually charged with a crime of sexual nature.

Appendix 14. Numbers of wapiti of each age group and sex removed* from Waterton Lakes prior to February, 1957

Year	<1 Yr.		≥1 Yr.		Total
	♂♂	♀♀	♂♂	♀♀	
1947-48	14	11	17	44	87†
1948-49	4	1	13	15	33
1957-58	?	?	?	?	97

* Shot in winter without deliberate selection.

† Includes one specimen of unidentified sex.

REPORT ON THE PROGRESS OF THE WORK DURING THE YEAR 1900

NAME		AGE		SEX	
1	2	3	4	5	6
7	8	9	10	11	12
13	14	15	16	17	18
19	20	21	22	23	24
25	26	27	28	29	30
31	32	33	34	35	36
37	38	39	40	41	42
43	44	45	46	47	48
49	50	51	52	53	54
55	56	57	58	59	60
61	62	63	64	65	66
67	68	69	70	71	72
73	74	75	76	77	78
79	80	81	82	83	84
85	86	87	88	89	90
91	92	93	94	95	96
97	98	99	100	101	102

THE FOLLOWING TABLES SHOW THE RESULTS OF THE WORK DURING THE YEAR 1900

Appendix 15. Wapiti of each year class and sex removed* from Elk Island, 1958 - 1963

Year class	Period of removal									
	Dec, '58		Nov, '59- Jan, '60		Dec, '60		Dec, '63		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1963							10	6	10	6
1962							8	8	8	8
1961							7	7	7	7
1960					4	13	4	8	8	21
1959			33	36	18	18	1	2	52	56
1958	2	15	44	30	3	7	4	5	53	57
1957	7	13	32	38	6	9	2	1	47	61
1956	19	11	20	50						
1955	10	11								
1954							1	1		
1953							1	4		
1952							2	2	74	245
1951							1	1		
1950										
1949										
Older†	14	43	7	98	2	20				
?‡	15	12	11	11	1	5			27	28
Total	67	105	147	263	34	72	38	49	286	489

* Shot without deliberate selection.

† Age ≥4 years when slaughtered, but not determined to year.

‡ Age not known, but carcass weight indicated age ≥1 yr.

Appendix 16. Numbers of wapiti of each year class and sex removed* from Jasper, December, 1957 to January, 1967

Year class	Period of removal						Total	
	Dec, '57- Jan, '58		Dec, '63- Jan, '64		Nov. '66- Jan, '67			
	♂	♀	♂	♀	♂	♀	♂	♀
1966					10	14	10	14
1965					22	10	22	10
1964					7	11	7	11
1963			9	19	7	18	16	37
1962			15	16	3	20	18	36
1961			5	21	5	12	10	33
1960			9	22	3	11	12	33
1959			2	12	2	4	4	16
1958			4	10		10	4	20
1957	2	7	3	15		8	5	30
1956	11	7	3	9		3	14	19
1955	4	9	1	5		2	5	16
1954	3	3	2	9	1	4	6	16
1953			1	3		1		
1952				1		2		
1951						1		
1950			1					
1949				1			11	33
1948				1				
1947								
1946				1				
Older†	9	22						
Total	29	48	55	145	60	131	144	324

* Shot without deliberate selection.

† Age ≥ 4 years when slaughtered, but not determined to year.

Appendix 17. Numbers of wapiti of each year class and sex, removed from Cascade and Red Deer drainages, Banff, 1960-66

Year class	Period of removal																															
	Dec, '60*		July, '61†		Nov, '61*		June, †		Dec, '62*		Dec, †		Dec, '63*		Dec, †		Dec, '64*		Dec, †		Aug, †		Nov, *		Nov, †		Nov, *		Total			
	Jan, '61		-May, '62		-Jan, '62		-Oct, '62		-Jan, '63		'62		-Jan, '64		'63		-Jan, '65		'64		-Oct, '65		-Dec, '65		'65		-Dec, '66					
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀		
1966																													7	1	7	1
65																					1			1	1	2	1			2	4	
64																	6	4		4	5			1	1					3	11	13
63													1		1	1	2	3		6	5							1	5	11	14	
62															13	16								1	3		1			21	28	
61				1		1	2	2	2						9	10		1	3	11		1		1	1			1		17	29	
60	2	2	7	5			7	2		1						6				1	1	3		3	1		2	1		21	24	
59	2	1	4	3	2		1		1								3	1	6					2	2			4		13	20	
58		5	1	1	1				1			4	1	1				2	4			1		5				1		7	20	
57		5		3		2	1		1	2		4		1					6					3				1		2	27	
56		1	3	1	1		1	1			1	7	1	1				1	5					4				2		8	22	
55		2	1	1	1	1						7						1	6		1			2				1		4	20	
54		1		1		2						1	1	1					2									1		1	9	
53	1			1					1			6		1					2		2							1		3	16	
52		4	1	1				1				3							2		3			1						1	15	
51	2	4	1									3																1		3	8	
50		†		1								1																				
49						1				1				1				1						1								
48		8				1																		2								
47						1						2																				
46												3													1							
45		†										1				1																
44		†						1				2																				
43				1																												
42		1																														
41							1																									
40																																
39		†																														
‡§	1	1		1		1															8		3	10	1	9				5	30	
Total	8	35	18	21	5	10	12	8	5	5	23	76	4	7	3	13	20	65	10	18	4	2	5	40	8	11	12	23	137	334		

*Shot without deliberate selection

†Shot selectively for research collection

‡Trapped without deliberate selection

§Age not known, body size indicated age ≥1 year

Deer drainages, Banff, 1960-66

*	Dec, ‡ '64		Aug, † -Oct, '65		Nov, * -Dec, '65		Nov, ‡ '65		Nov, * -Dec, '66		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
									7	1	7	1
				1		1	1	2	1		2	4
4	5					1	1			3	11	13
6	5								1	5	11	14
						1	3		1		21	28
				1		1	1			1	17	29
						3	1		2	1	21	24
					2	2				4	13	20
		1				5				1	7	20
						3				1	2	27
						4				2	8	22
		1				2				1	4	20
										1	1	9
		2				2				1	3	16
						1					1	15
										1	3	8

						1					} 0 34	
						2						
						1						

	8				3	10	1	9			5	30

10	18	4	2	5	40	8	11	12	23	137	334	

Appendix 18. Numbers of wapiti of each year class and sex, removed* from Bow Valley, Banff 1957-1966

Appendix 18. Numbers of waders																									
Year class	Period of removal																				Total				
	Nov,- Dec,'57		Dec,'58 -Jan,'59		Dec,'59 -Jan,'60		Dec,'60 -Jan,'61		Oct,'61		Nov,'61 -Jan,'62		Dec,'62 -Jan,'63		Dec,'63 -Jan,'64		Dec,'64 -Jan,'65		Nov,'65				Nov,- Dec,'66		
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
1966																						3	1	3	1
65																					5	4	5	4	
64																					2	4	8	13	
63														4	9	10	4				2	2	14	15	
62													10	7	7	3	1	6			2	2	20	18	
61											19	10	8	9	8	6	1	4				2		36	31
60							10	8	2		16	12	5	8	6	2		3				1		39	34
59					27	17	13	18			6	21	4	9	3	2		1		1				54	69
58			7	9	12	13	7	9			2	18	4	4	1	1		6						33	60
57	4	5	6	9	9	31	4	16			5	12	7	1	2	1		2				1		37	78
56	12	7	4	9	13	18	4	13			3	9	2	2	3	1		2				1		41	62
55	4	7	0	4	18	25	3	16			2	10	3	1	2	2		4						32	69
54	3	6			11	18	2	3			2	10		2	2			1				1			
53					4	15	1	1				5	1	1		2		1							
52					3	9	4	3			4	4	2			2									
51					6	10	1	3			1	4		1	1			1							
50					5	10	†	†				2		1		1		1							
49					†	†						1	1	1				3							
48							3	5				1		2		1		1							
47					1	8					2	4				1									
46												3		1											
45							↓	↓				1													
44					↓	↓		†				1													
43					†	†						1													
42								2				1													
41					1	3																			
40								↓																	
39					↓	↓																			
38																									
Older†	10	21	20	31																					
‡	4	8			10	3	1	1			2	3	1	2										18	17
Total	37	54	37	62	120	180	53	98	2		64	133	48	52	39	34	18	49	1		12	20	431	682	

* Shot. Animals collected October 15, 1961 and November 19, 1965 were selected as to sex and age.

In slaughters of December, 1964 to January, 1965, and November to December, 1966, shooting of bulls was avoided.

In all other slaughters there was no deliberate selection.

† Age ≥4 years when slaughtered, but not determined to year.

‡ Age not known, but carcass weight indicated age ≥1 year.

nff 1957-1966

Dec, '64 Jan, '65		Nov, '65		Nov, - Dec, '66		Total	
♂	♀	♂	♀	♂	♀	♂	♀
				3	1	3	1
				5	4	5	4
6	9			2	4	8	13
10	4				2	14	15
1	6			2	2	20	18
1	4				2	36	31
	3				1	39	34
	1	1			1	54	69
	6					33	60
	2				1	37	78
	2				1	41	62
	4					32	69
-----					1		
	1						
	1						
	1						
	1						
	3						
	1						
						> 91	211
						18	17
18	49	1		12	20	431	682

x and age.

ting of bulls was avoided.

Appendix 19. Numbers of wapiti of each year class and sex removed* from Waterton Lakes, November, 1958 to February, 1963

Year class	Period of removal						Total		
	Nov, '58- March, '59		Nov, '59- Jan, '60		Dec, '62- Feb, '63				
	♂	♀	♂	♀	♂	♀	♂	♀	
1962					11	12	11	12	
1961					10	15	10	15	
1960					1	13	1	13	
1959			14	23	2	8	16	31	
1958	7	14	19	13	1	6	27	33	
1957	35	7	3	13	2	9	40	29	
1956	19	10	5	13		11	24	34	
1955	5	22				3	}	46	130
1954						3			
1953					1	2			
1952						4			
1951						2			
1950									
1949						2			
1948									
1947						1			
Older†	29	40	11	51					
‡#	6	1	1	1		3	7	5	
Total	101	94	53	114	28	94	182	302	

* Taken without deliberate selection, by shooting and trapping.

† Age ≥ 4 years when slaughtered, but not determined to year.

‡ Age not known but carcass measurements indicated age ≥ 1 yr.

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